HELMINTHS OF THE PARADISE SHELDUCK *TADORNA VARIEGATA* (GMELIN) IN THE HIGH COUNTRY OF CANTERBURY

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THESIS

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"Host and parasite have often been studied as separate entities, although it is only by studying both animal populations that knowledge of this intimate relationship can be of greatest value."

Sharpe (1964)

ABSTRACT

The helminth parasites of the gastro-intestinal tract of the Paradise Shelduck *Tadorna variegata* (Gmelin) are surveyed together with aspects of the shelduck's ecology (particularly food and feeding habits). Twenty-two species of helminth parasite (19 from the gastro-intestinal tract), including one new species of notocotylid, are recorded from 281 shelducks examined. Their normal locations are noted. The new species is described and an account of its life history is given. The life history of a second notocotylid species, *Uniserialis gippyensis,* is described for the first time and the New Zealand intermediate host of a cosmopolitan cestode, *Cloacotaenia megalops,* is identified. Present knowledge of the life histories of all other helminth species found in the Paradise Shelduck is reviewed, and probable New Zealand intermediate hosts are suggested. Quantitative aspects of the helminth infections are examined, and comparisons made between burdens of adult and juvenile hosts, and males and females. Seasonal fluctuations in levels of infection are discussed. For comparison with the shelducks, helminth fauna and food of "dabbling ducks" and geese from the study area are investigated. The host-parasite-environmental inter-relationships are discussed in an attempt to explain the composition and dynamics of the shelduck's helminth fauna. A brief discussion of pathology is included.

CHAPTER I

GENERAL INTRODUCTION

Generally, waterfowl are vulnerable to a much richer platyhelminth fauna than most other groups of birds because of their association with aquatic environments. Probably for this reason the parasites of waterfowl have been fairly extensively studied over the last century. These studies have been recorded in several very thorough, annotated, bibliographies, the most recent of which are those by Lapage (1961) and McDonald (1969). Virtually all of this work has been carried out in the Northern Hemisphere, and until recently much of it was either of a descriptive nature, or dealt primarily with pathology. There have been relatively few studies which consider the factors influencing the composition and dynamics of the parasite fauna of waterfowl species. The most extensive of these studies have been carried out in eastern Europe and the U.S.S.R., where parasites of wild ducks and other waterfowl are considered a threat to the establishment of poultry farms.

There has been a marked lack of research on the parasites of the many waterfowl species of the Southern Hemisphere. Until recently, the only work published on the endoparasites of New Zealand's several species of waterfowl, was an account of an experimental infection of a New Zealand Scaup *Aythya novaeseelandiae* with a schistosome trematode *Cercaria longicauda* (MacFarlane, 1949). No adult trematodes were found, although schistosome eggs were passed by the duck.

A study by Rind (1974) is the only recent work to have been published on parasites of New Zealand's waterfowl. In this she surveyed trematodes of several waterfowl species in New Zealand. Thirteen genera of trematodes belonging to the families Notocotylidae, Echinostomatidae, Strigeidae, Schistosomatidae, Microphallidae, Psilostomatidae, Cyclocolidae and Opisthorchiidae were recorded. The presence of cestodes of the family Hymenolepididae and nematodes of the families Ascaridae, Spiruridae and Trichuridae was mentioned, and acanthocephalans were found in hosts collected from estuarine areas.

Six helminth species listed by Lapage (1961) from the New Zealand Grey Duck *Anas superciliosa superciliosa*, *viz.* *Echinostoma revolutum*, *Notocotylus attenuatus*, *Diorchis acuminata*, *D. flavescens*, *Diploposthe laevis* and *Fimbriaria fasciolaris* are all erroneous records. Except for *Diorchis acuminata*, these species were actually found in the Australian Black Duck *Anas superciliosa rogersi* (recorded by the authors cited by Lapage simply as *Anas superciliosa*). McDonald (1969) found that the presence of *D. acuminata* in Lapage's list was also an erroneous citation.

Apart from four trematode species, *viz.* *Uniserialis gippyensis*, *Catatropis* sp. *Echinoparyphium recurvatum* and *Echinostoma revolutum*, recorded by Rind (1974), the helminth fauna of the New Zealand Paradise Shelduck *Tadorna variegata* (Gmelin) was unknown.

The present study was undertaken in an endeavour to discover the range of helminth parasites which infect the Paradise Shelduck in its natural habitat, to elucidate the dynamics of the helminth fauna and to relate this, where possible, to the ecology of the host species and the life cycles of the helminth species involved.

The study is based on a total of 281 Paradise Shelducks collected mainly from the highcountry of Canterbury. For comparative purposes, the endoparasites of six Grey Ducks, one Mallard and two Canada Geese from the study area, were also examined.

CHAPTER II

STUDY AREA

Of the 281 Paradise Shelducks examined during this study, 250 were shot in the main study area on the Canterbury side of the Lewis Pass, *viz.* the valleys of the Hope, Kakapo, Doubtful and Boyle rivers. The above rivers are all interconnected and flow into the Waiau River as the Hope River (Fig. 1). The river valleys in this area are typical of the habitat favoured by Paradise Shelducks in Canterbury. They consist of wide, open, shingle riverbeds bordered by grassed riverflats and terraces (Fig. 2). The valley sides are in the main covered by indigenous beech forest (*Nothofagus fusca* and *N. solandri*). The rivers are rocky and waterflow is swift (Fig. 3). This allows little development of plant or animal life in the main channels. Frequent slower flowing creeks and backwaters are associated with this type of river and these usually contain a greater abundance of aquatic life (Figs. 4 & 5). Occasional areas of swamp occur on the riverflats during the spring and winter, but many of these are dry during the summer and autumn. Three small but permanent lakes are also present.

Climate in this area is harsh compared to lowland areas of Canterbury. During the summer the weather is typically hot and dry, and in the winter severe frosts are not uncommon, causing most still and gently flowing waters to freeze over (often for many days in succession). These quieter waters are therefore often relatively inaccessible to waterfowl during much of the winter.

Due to farming activity, there has been a considerable increase in the acreage of exotic grasses, clovers, lucerne, and other fodder crops such as turnips over the last 10 years. Much of the terrace-land, particularly above the Hope River, has been cultivated and sown in these exotics, but large areas of indigenous tussock grassland still remain.

During the study four other species of waterfowl were seen inhabiting the study area, *viz.* Grey Duck (*Anas*

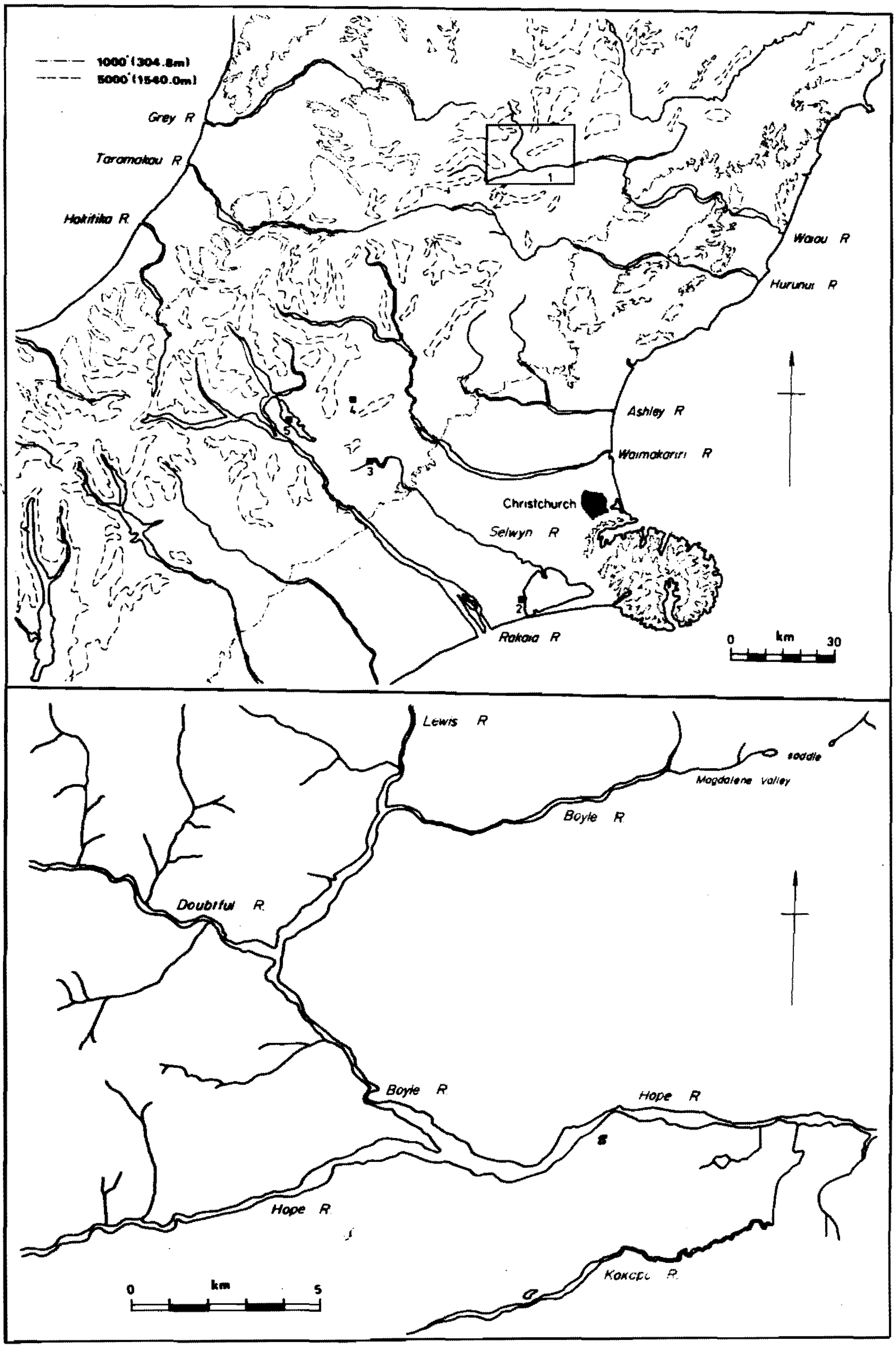


Figure 1. Study area. Above: Locations from which shelducks were obtained - 1. Main study area, Lewis Pass; 2. Lake Ellesmere; 3. Selwyn River; 4. Porter's Pass; 5. Lake Coleridge. Below: Main study area, Lewis Pass.

Figure 2. Typical high-country riverbed habitat of the Paradise Shelduck - Kakapo River.

Figure 3. Main channels on such riverbeds are swift and rocky, showing little development of aquatic life.

Figure 4. Backwater on the bed of the Doubtful River. Frequent backwaters are present on most Canterbury high-country riverbeds.

Figure 5. Vegetation in a typical backwater. Aquatic plant and animal life is usually abundant in such backwaters.

superciliosa superciliosa), Mallard (*Anas platyrhynchos platyrhynchos*) and Canada Goose (*Branta canadensis*) were common, and a pair of New Zealand Scaup (*Aythya novae-seelandiae*) were seen on one of the lakes in the area in February 1973. Other birds commonly seen associated with water in the study area were Spurwinged Plover (*Lobibyx novaehollandiae*), Little Shag (*Phalacrocorax melanoleucos*), Black-backed Gull (*Larus dominicanus*) and Pied Oystercatcher (*Haematopus ostralegus finschi*).

The remaining 31 shelducks were collected from the headwaters of the Selwyn River, Lake Coleridge, Porters Pass and Lake Ellesmere. With the exception of Lake Ellesmere, which is coastal and slightly saline, the other areas from which birds were obtained provide similar shelduck habitats to those of the main study area. All these areas lie at similar altitudes along the base of the Southern Alps in Canterbury and thus the climate is also similar.

Details of the dates and locations of all birds examined in the study are given in Appendix 1. Seventy seven of the birds were collected from licensed shooters during the legal shooting season in 1971 as part of a pre-thesis project (Bisset, 1971). Most of the remaining birds were collected during the legal shooting seasons (May) of 1972 and 1973, again from licensed shooters, but 10 birds per calendar month were shot by me between June 1972 and March 1973 inclusive, under a permit issued by the Wildlife Division of the Department of Internal Affairs.

CHAPTER III

THE DEFINITIVE HOST - PARADISE SHELDUCK

I. INTRODUCTION

The Paradise Shelduck is New Zealand's only indigenous shelduck species. It now has a fairly widespread distribution throughout the country, though it is probable that in pre-Polynesian times the species distribution was limited by the availability of suitable grassland habitats (Williams, 1971). However, reduction of forests and introduction of exotic pasture plants have allowed the species to extend its distribution particularly in the North Island, although exploitation by shooters has kept the numbers low (McAllum, 1965). In Canterbury at present, Paradise Shelducks are distributed mainly throughout the foothills of the Southern Alps, though smaller numbers occur throughout most of the province, particularly near rivers in areas not intensively farmed. Unfortunately apart from anecdotal records, little has been published regarding their general biology. However, the Wildlife Division of the Department of Internal Affairs is at present undertaking research into aspects of the species biology.

A basic knowledge of the host's ecology is essential before a good understanding of the dynamics of its parasite fauna can be acquired. Parasitic helminths of the alimentary tracts of waterfowl species almost invariably enter their hosts via the mouth, so infection depends to a very large extent on the feeding habits of the host species. Therefore, a detailed consideration of the diet of the Paradise Shelduck was considered to be essential in this study. However, other aspects of the shelduck's overall biology also have a considerable influence on the composition and dynamics of the parasite fauna. Ideally, aspects such as age, sex, mobility, breeding biology, behaviour, physiology, seasonal changes to habitat and relationships with other waterfowl species should all be considered in a study such as this. Very little is known about most of these aspects of the shelduck's biology, and because the undertaking of any detailed work of this sort is beyond the scope of this study, aspects other than feeding are dealt with only briefly.

II. COLLECTION OF SAMPLES

Most of the Paradise Shelducks collected during the shooting seasons of 1971, 1972 and 1973 were obtained from a number of licensed duck shooters hunting within the North Canterbury Acclimatisation Society's district. Those collected outside these seasons were shot under permit by myself. A Labrador retriever was used to reduce to a minimum any loss of wounded birds. Appendix 1 gives details of where and when ducks were obtained.

Once shot each bird was labelled with a number, exact location from which it was obtained and whether it was solitary, or one of a pair or group. The alimentary tracts of all birds were removed as soon as possible, and with the exception of those collected in the 1972 shooting season, all tracts were examined fresh. The large size of the sample from the 1972 season meant that most of this material had to be frozen and examined when time permitted. To give an indication of physical condition the gutted weight of each bird was recorded in the laboratory as was the weight of fat from within the abdominal cavity. The presence or absence of the bursa of Fabricius was noted, and when present its length was measured. In addition to recording information about the shot birds, notes were kept of numbers and locations of birds seen during each sampling trip.

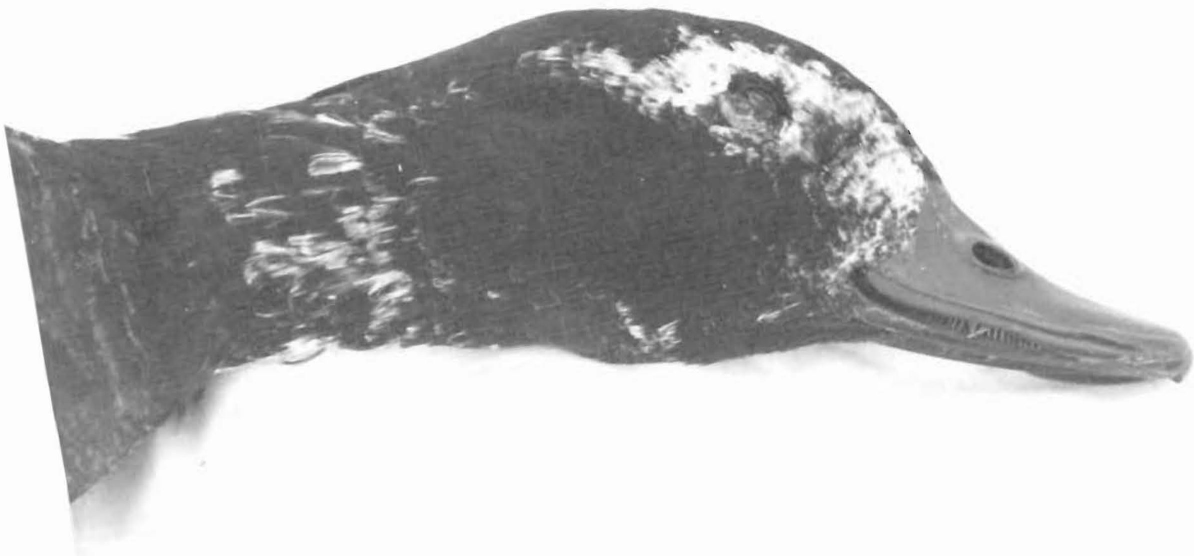
III. SEXING AND AGEING

Sexing of Paradise Shelducks is generally easy because of the sexual dimorphism in colour - basically the female is brown with a white head while the male is completely black. However, in the juvenile birds this dimorphism appears only a short time before they can fly and so with birds before this stage, sexing could be carried out only by dissection. In these cases the syrinx was checked as a quick indication in the field. This organ, which is an enlargement of the trachea at its junction with the two major bronchi, is present only in males of most duck species (Hess, 1951). Its development begins at an early age. Sexes of all birds were re-checked in the laboratory by dissection. One bird, taken in May 1971, which had a mottled head with similar amounts of black and white, proved on dissection to be a male. A second male with a mottled head was shot during the duck season of 1973 (Fig. 6).

Ageing birds of any species is difficult and it was found that only two broad age classes could be separated for *T. variegata* - these being designated "adults" and "juveniles". The shelducks were divided into these two age classes according to the presence or absence of a bursa of Fabricius. This criterion has been used frequently to age birds - particularly gamebirds. As a general rule the bursa increases rapidly in size in young birds until the time when the sex cells are just begining to divide. It then gradually diminishes (Taber, 1971). Ward and Middleton (1971) found for the Mallard, that by the age of 40 weeks the bursa had all but disappeared. However, in other species such as geese, sexual maturity is often not reached in the first year, and so the regression of the bursa is more gradual (Taber, 1971).

No study has been made of the regression of the bursa of the Paradise Shelduck. Coster (1972) stated that the Paradise Shelduck is normally three years old before breeding commences. However, it is probable that many breed, or at least attempt to breed, before this age, particularly at low population densities. It is therefore uncertain what ages are denoted by the presence or absence of a bursa. Indications are that the bursa regresses over a period of about 12 months, by which time it has been virtually lost. If the regression took longer, two size classes of bursa could have been expected in the shelduck population simultaneously for a large part of the year. There was no evidence of this. Throughout the study, only one size class of bursa was

Figure 6. Head of male Paradise Shelduck showing abnormality of colouring. Shelducks with similar abnormalities are sometimes mistaken for juvenile females.



present in the shelducks for all but a very short time (November-December).

In May 1972 the bursae of the juvenile shelducks ranged between 25-40 mm in length (measurements were taken after dissection, from the tip of the bursa to the entrance into the cloaca). By September the average length of the bursae of six juvenile birds in the sample was 18 mm (S.D. 4). The bursae were even more reduced in overall bulk than was indicated by their length. In May the bursae were large fleshy and conspicuous, but by September-October they had become rather inconspicuous and lay close to the wall of the cloaca. By November-December all that remained of the bursae were little more than small thin-walled pockets in the wall of the cloaca. By this time young ducklings were present in the population. The average bursa length of two male ducklings obtained in November at approximately one month old was 35 mm and the average of two males obtained in December at two to three months old was 38 mm. It therefore seems valid to assume that the birds which possess conspicuous bursae are one year old or less.

IV. BEHAVIOURAL ASPECTS OF THE SHELDUCK'S ECOLOGY

1) Flocking

Flocking of Paradise Shelducks is seen throughout the year. During autumn in the study area, large flocks graze on exotic pasture. McAllum (1965) referred to these as "post-moulting flocks". In the study area they were often seen up to two kilometres from the nearest body of water. Virtually all birds shot during the shooting season (May), were taken from such flocks. These flocks consist mainly of birds of the year (aged about six months), and so McAllum's term may be misleading as most of the flock birds would therefore not have moulted. Of those collected on the opening weekends of the duck seasons of 1971 and 1972, 78% and 73% respectively possessed large bursae of Fabricius. It is thought likely that most of the remainder of the birds collected from these flocks were 18 months old unpaired birds. While most of the birds seen at this time of the year were in flocks, a considerable number remained in pairs unattached to the flocks. These birds were more often seen in riverbeds or small swampy areas in the study area than feeding on cultivated pasture, and they rarely associated closely with other pairs. It is believed that many pairs remained in or near their breeding territories throughout most of the autumn and winter. This supports the view held by Zander (1967) that the ecological niche occupied by the species is divided into two separate "subniches", one for the breeding population and one for the non-breeding population. Flocks tended to be broken up and scattered somewhat by the disturbance of the shooting season. In June, July, and August 1972, flocks of 30-40 were the largest seen, but many scattered smaller flocks were present.

2) Breeding

By September a flock of approximately 100 birds was present feeding on the exotic pasture in the study area. Smaller groups on the riverbeds and unimproved land were less frequently encountered, but paired birds were widely dispersed on riverbeds and swampy areas with a good plant cover. They tended to be aggressive towards other shelducks which landed near, often flying over 200 metres to drive them off. This behaviour may account for the formation of larger flocks on areas unsuitable for nesting. McAllum (1965) called these "non-breeding flocks".

The first two broods of young shelducks were seen during October. Both broods, each containing seven shelducklings, when found, were feeding in sheltered slow-flowing backwaters, but quickly made for the main channel when disturbed. The following month on the same territories, two shelducklings remained on one brood while all those in the other appeared to have died although the adults still occupied the territory. The largest shelduck brood seen during the study numbered 11. The last non-flying juveniles were seen during December, but a brood of newly hatched young seen in late November would not have flown until at least the end of January.

3) Moulting

In late summer all shelducks apart from the young of the year undergo a moult. During their moult they congregate on lakes and so reduce the risk of predation while they are flightless. In the study area two lakes were used by moulting flocks. Approximately 300 birds were moulting in January on the larger of the two (approximately 150 m by 300 m), while 17 were moulting on the smaller one (approximately 40 m by 80 m). By the end of February the moulting flock on the larger lake consisted of only 63 birds and none were present on the smaller one. By late March no moulting birds were present on either lake.

4) Mobility

Although Paradise Shelducks are strong fliers, it appears that the adult birds are comparatively sedentary (Dr M. Williams, pers.comm.). Most of their dispersal (and thus that of their parasites) is probably carried out by young birds seeking new feeding areas or territories. Thus, while the helminth fauna of most of the adult shelducks is likely to have been obtained in fairly close proximity to where the birds were shot, this assumption may not be true for many unpaired or juvenile birds.

5) Relationships with other waterfowl

Delacour (1963) reported that in captivity *T. variegata* can be antagonistic to other species of waterfowl. In the study area however, they appear to associate freely with other types of waterfowl. Paradise Shelducks were seen on several occasions grazing amongst Canada Geese, and often occupied ponds with Grey and Mallard Ducks and geese. No antagonism was seen between the different species. Thus, there are probably frequent opportunities for interchange of parasites to occur between these waterfowl species.

V. PHYSICAL CONDITION

During the present study no shelduck collected was in an emaciated condition. Nevertheless, an indication of the physical condition of the shelducks examined for parasites was considered to be desirable. During the shooting season (May) of 1972, where possible, the fatness of the birds in the sample was estimated visually from the size of the internal fat deposits and ranked on a 1-5 scale. However, from July 1973 until the end of the study a more objective measure was adopted. A fat index was chosen as this measure.

Riney (1955) discussed the use of fat as an indicator of condition and compared various indices in evaluating physical condition of Red Deer (*Cervus elaphus*). He concluded that the most satisfactory index in the case of deer was one which he termed the "kidney fat index". This was obtained by expressing the weight of the perinephric fat as a percentage of the kidney weight (which he considered proportional to the body weight). Flux (1971) pointed out that fatness is not necessarily a direct indicator of condition as seasonal changes in fat deposits are normal. Nevertheless, an indication of condition can be obtained by comparing fat indices of similar individuals at the same time.

Cornwall and Cowan (1963) in considering the pathological effect of parasites on the Canvasback Duck (*Aythya valisineria*), used their "emaciation index" to compare physical condition of the birds. This index was calculated by dividing the keel meat depth by the keel depth.

There appears to be a much larger margin of error involved in measuring the "emaciation index" and consequently a fat index was used during the present study.

The Paradise Shelduck has two conspicuous fat deposits within the abdominal cavity - one lies directly underneath the abdominal muscles and the other alongside the alimentary tract amongst the mesenteries. Because the range of weights was greater for the subabdominal deposit, it was easily removed without loss, and was not complicated by the added weight of mesenteries, the index used was based on the weight of the subabdominal fat deposit and the eviscerated body weight-fat weight x 100/body weight.

Juvenile birds collected during the shooting seasons were in general noticeably fatter than adult birds. They could generally be separated from the adult birds quite simply without dissection by the larger amount of subcutaneous fat. Thirty two juvenile birds collected on May 6-7 1972, whose condition was estimated visually and ranked on a 1-5 scale, averaged 4.6 on this scale, while 10 adult birds in the same sample averaged only 3.3. In addition, in a sample of 10 birds collected on May 5-6 1973, three juvenile birds possessed an average fat index of 2.39 (S.D. 0.45), while the average index for the remaining seven adult birds was 0.59 (S.D. 0.40). Fat and body weight data are included in Appendix 2.

Table 1. MONTHLY VARIATION IN THE FAT INDICES OF ADULT SHELDUCKS.

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	May
No. of adults in sample	7	8	4	5	7	8	9	9	10	7
Average fat index	0.31	0.67	0.60	0.19	0.22	0.37	1.06	0.18	0.49	0.59

The monthly variation in the fat index of adult shelducks is shown in Fig. 7, derived from data in Table 1. The fluctuations in average fatness of adult shelducks shown in this graph can in general be explained by various annual events in the biology of these birds. Throughout the winter most adult shelducks are fairly fat with the odd exceptionally fat individual being present. These latter individuals have internal fat deposits of a size more characteristic of juvenile birds and when present in a sample they tend to raise the average measurement considerably. By October-November (the onset of breeding), the birds have in general lost much of their fat, but the deposits grow again as the shelducks approach their moult.

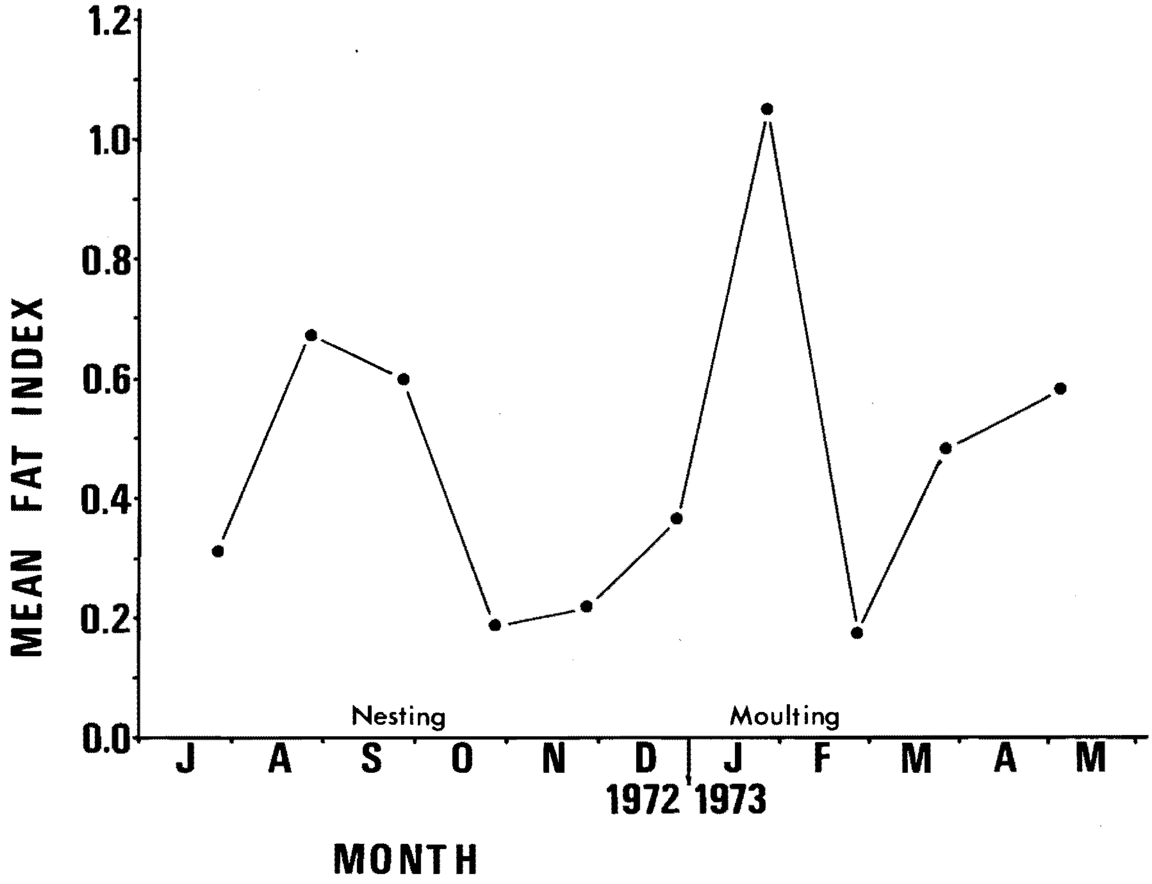


Figure 7. Monthly variation in the fat indices of adult shelducks.

In January many shelducks are flightless due to this moult. Those in the January sample which were taken while flightless had exceptionally low fat reserves, and their body weights were also very low, while those which had not begun their moult were exceptionally fat. These very fat birds are responsible for the dramatic rise in the average fat index for that month. By the end of February, most adult shelducks have either finished moulting or are nearly finished, and hence their fat reserves are probably at their lowest annual level at this time. Their fat reserves build up once more during the autumn.

Once birds are fully fledged their parasite load does not normally appear to be detrimental to their physical condition. No obvious relationship was seen between condition of fully fledged birds and their parasite loads. Generally the population as a whole appears to be most heavily infected with helminths at the time of the year when its members are fattest (see Chapter VI). The simultaneous rises in these parameters during the autumn are probably independent.

Shelducklings appear to carry little or no fat up to at least one month of age. Two one month old shelducklings taken in November, possessed no internal fat deposits. Another young bird of approximately twice this age taken in December (which was within approximately one week of flying), possessed a fat index of 0.41, while a second, newly flying, juvenile taken in the same sample which had a much larger burden of helminths (see Appendix 2, No. 155), was rather thin and had a fat index of only 0.11. A fifth juvenile in January, which was also newly flying, had a fat index of 0.37 and possessed a moderate helminth burden (see Appendix 2, No. 165).

There appears to be a possibility that in juvenile shelducks, prior to complete independence from their parents, a relationship between condition and helminth burden may exist, but there is insufficient data available at this stage to draw any more definite conclusions.

VI. FOOD AND FEEDING HABITS

Although it is well known that the Paradise Shelduck is basically a grazing species - Travers (1871), Oliver (1955), McAllum (1965), and Williams (1971) - it appears that no study has been carried out to determine the extent of its grazing habit. While such a study is of great interest in its own right, it has been included in this thesis primarily to indicate ways and means by which the Paradise Shelduck acquires its helminth parasite burden. This section is based on data from 204 shelducks taken between May 1972 and May 1973 inclusive.

1) Methods

While the gut contents were being scanned for gut parasites, identifiable pieces of food material were also searched for. In general such material was in or anterior to the gizzard. Those pieces which could not be identified immediately were stored in 10% formalin in labelled vials for later analysis. Food material which could be identified immediately was not stored but the species or category present was recorded. No quantitative estimates of the foods eaten were recorded. Proportions of the various foods in the diets of the ducks are instead expressed simply as percentage occurrence throughout the sample. Healy (1970), Allan (1940), and Mason (1964) were consulted for identification of plant material, and Marples (1962) and Pendergrast and Cowley (1966) for animal material. Representative examples of a number of unidentified seeds and some vegetative material were kindly identified by Mrs M. Bulfin of Botany Division, DSIR, and Dr M. Winterbourn of the Zoology Department, University of Canterbury identified many of the aquatic insects.

2) Results

a) Overall Composition of Diet - Of the 204 birds examined, 202 contained identifiable foods. Of these 201 contained plant material, and 72 contained animal material.

i) *Animal material.* None of the invertebrate species which had been eaten by the Paradise Shelducks occurred commonly in the diet (Table 2). Even when present animal material contributed very little to the bulk of the food. Once ingested, soft-bodied invertebrate species are broken down into an unrecognisable form much more quickly than are species with hard parts (such as caddis flies or snails), or plant material. Due to the different rates of breakdown of different food items, there is a tendency to underestimate the occurrence of soft-bodied food items (Coleman, 1972). However, despite this, it is clear that the shelducks rely very little on food material of animal origin for their nutrition.

With the exception of *Dorylaimus* sp., a species of free-living nematode, all invertebrate food species which were recovered on more than one occasion were aquatic in origin. Aquatic larval stages of various insects (particularly those of caddis flies), were the most commonly encountered, being present in 28.4% of the shelducks examined. The larvae of *Oxythira albiceps*, a caddis fly, was the most commonly ingested animal food, and was the only animal species which occurred in over 15% of the birds.

Although 11 terrestrial and free-flying species were identified from the birds, none was recovered from more than one bird. Most were adult forms of the aquatic insect larvae found in the birds.

Undoubtedly, in many cases, animal material was taken in accidentally along with plant foods. The presence of aquatic invertebrates was generally associated with the simultaneous presence of filamentous algae or other aquatic plant material. Marples (1962) stated that *Oxythira* spp. in particular, are found amongst filamentous algae. Many of the other species of aquatic invertebrates found also seek the shelter of this alga (Pendergrast and Cowley, 1966). *Dorylaimus* sp., which was the most frequently found animal species after the caddis fly larvae, lives amongst terrestrial vegetation (Dr W.C. Clark, pers. comm.). The small size of these nematodes makes it most unlikely that they were eaten intentionally.

However, several of the shelducks had clearly been intentionally seeking animal food. Eight of the 10 birds collected from the headwaters of the Selwyn River in May 1972 contained particularly large numbers of caddis fly larvae. *Olinga ferridayi* and *Pycnocentrodes aureola* made up the bulk of food in the oesophagus and gizzard of these ducks, and they were not associated with the presence of aquatic plant species. Of their natural distribution Pendergrast and Cowley (1966) said that both species are mainly found in stony parts of streams in moderately flowing water, although sometimes also in aquatic vegetation. While some of the free-flying and terrestrial species (e.g. ant and booklice) were probably ingested accidentally, others found, such as the mayfly and damselfly adults and a moth, may well have been eaten intentionally.

A further six shelducks contained small amounts of "aquatic detritus" - a mixture of semi-decomposed root and stem material of aquatic plants. A number of ingested aquatic invertebrates, such as molluscs (*Sphaerium novaezelandidae, Potamopyrgus antipodarum* and *Lymnaea tomentosa*), crustaceans (cladocerans and ostracods) and insect larvae, were always associated with this material. While these species were also often present with ingested filamentous algae, their presence with "aquatic detritus" (particularly in the case of *S. novaezelandiae* and the crustaceans), suggests a "dabbling" type of feeding behaviour more characteristic of *Anas* spp.

Oligochaetes were not found in the tracts of the shelducks. Once ingested these are broken down very quickly and their presence is often indicated only by their setae. Setae were not searched for. Nevertheless, it is likely that aquatic oligochaetes are ingested frequently with other food material, and it is thought that earthworms are probably eaten occasionally when conditions are suitable. Such conditions exist immediately after rain when earthworms are forced to the surface in poorly drained areas. Paradise Shelducks have also been

Table 2. FOOD SPECIES FROM THE TRACTS OF 204 PARADISE SHELDUCKS COLLECTED BETWEEN MAY 1972 AND MAY 1973.

		N*	%*
TERRESTRIAL - VEGETATIVE			
MUSCI (mosses)			
	Breutelia affinis	2	1.0
DICOTYLEDONES			
Leguminosae	*Medicago sativa* *Trifolium dubium* *T. repens* *T. subterraneum*	132	64.7
Epacridaceae	*Cyathodes fraseri*	2	1.0
Polygonaceae	*Muehlenbeckia axilaris*	5	2.5
	Rumex acetosella	14	6.9
Plantaginaceae	*Plantago lanceolata*	1	0.5
Rosaceae	*Acaena* sp.	3	1.5
Rubiaceae	*Nertera depressa*	1	0.5
Umbeliferaceae	*Oreomyrrhis* sp.	5	2.5
	Anisotome aromatica	1	0.5
Caryophyllaceae	*Colobanthus* sp.	1	0.5
Compositae	*Hypochaeris* sp.	14	6.9
	Taraxacum officinale	14	6.9
	Cotula sp.	1	0.5
	Achillea millefolium	3	1.5
Salicaceae	*Salix fragilis*	1	0.5
Haloragaceae	*Haloragis (depressa?)*	1	0.5
MONOCOTYLEDONES			
Juncaceae	*Juncus* spp. (probably mainly *articulatus*)	42	20.1
Gramineae	including:		
	Lolium perenne *Poa pratense* *Anthoxanthum odoratum*	114	55.9

Table 2 (continued)

		N*	%*
TERRESTRIAL - SEEDS AND "BERRIES"			
DICOTYLEDONES			
Leguminosae	*Trifolium repens* *T. subterraneum*	23	11.3
Epacridaceae	*Cyathodes fraseri*	9	4.4
Polygonaceae	*Muehlenbeckia axilaris*	31	15.2
Haloragaceae	*Gunnera dentata*	8	3.9
Umbeliferaceae	*Lilaeopsis* sp.	1	0.5
Ericaceae	*Gaultheria depressa*	1	0.5
Rhamnaceae	*Discaria toumatou*	1	0.5
Araliaceae	*Pseudopanax crassifolium*	1	0.5
Cornaceae	*Corokia cotoneaster*	2	1.0
Lobeliaceae	*Pratia angulata*	1	0.5
Rubiaceae	*Coprosma* spp.	4	2.0
Rosaceae	*Rubus cissoides*	1	0.5
MONOCOTYLEDONES			
Junaceae	*Juncus* spp. (probably mainly *articulatis*)	12	5.9
Cyperaceae	*Scirpus* spp.	47	23.0
	Undet. sedge seeds *Carex* spp.	9	4.4
Graminaceae	*Poa pratense* Undet. grass seeds	12	5.9
	Avena sativa	11	5.4
AQUATIC PLANTS - VEGETATIVE			
CHLOROPHYTA			
	Oedegonium sp. *Mougetia* sp. *Ulothrix* sp.	43	21.1

Table 2 (continued)

		N*	%*
MUSCI			
Amblystegiaceae	*Drepanocladus aduncus*	10	4.9
DICOTYLEDONES			
Ranunculaceae	*Ranunculus fluitans*	7	3.4
MONOCOTYLEDONES			
Hydrocharitaceae	*Elodea canadensis*	1	0.5
Lemnaceae	*Lemna* sp.	3	1.5
AQUATIC PLANTS - SEEDS			
DICOTYLEDONES			
Potamogetonaceae	*Potamogeton cheesemani*	9	4.4
AQUATIC PLANTS - "AQUATIC DETRITUS"		6	2.9
ANIMAL MATERIAL - TERRESTRIAL OR FREE-FLYING			
NEMATODA			
	Dorylaimus sp.	16	7.8
INSECTA			
O. Psocoptera	Family undet.	1	0.5
O. Hymenoptera			
Formicidae		1	0.5
O. Diptera			
Simulidae	*Austrosimulium* sp.	1	0.5
Blepharoceridae	genus undet.	1	
Empididae	"	1	0.5
Undet. family		2	1.5
O. Hemiptera			
Saldidae	"	1	0.5

Table 2 (continued)

		N*	%*
O. Coleoptera			
Elmidae	"	1	0.5
O. Ephemeroptera			
Leptophlebiidae	*Deleatidium* sp.	1	0.5
O. Odonata			
	Xanthocnemis zelandica	1	0.5
ANIMAL MATERIAL - AQUATIC			
MOLLUSCA			
Hydrobiidae	*Potamopyrgus antipodarum*	8	3.9
Lymnaeidae	*Lymnaea tomentosa*	2	1.0
Planorbidae	*Gyraulus corinna*	3	1.5
Sphaeridae	*Sphaerium novaezelandiae*	5	2.5
CRUSTACEA			
O. Cladocera	2 undet. genera	2	1.0
S.C. Ostracoda	*Herpetocypris pascheri*	10	4.9
ARACHNIDA			
O. Acarina			
Halacaridae	genus undet.	2	1.0
INSECTA			
O. Ephemeroptera			
Leptophlebiidae	*Deleatidium* sp.	3	1.5
O. Plecoptera			
Gripopterygidae	*Megaloptoperla* sp.	1	0.5
	Zelandobius sp.	5	2.5
O. Trichoptera			
Rhyacophilidae	*Hydrobiosis* sp.	1	0.5

Table 2 (continued)

		N*	%*
Sericostomatidae	*Pycnocentrodes aureola*	21	10.3
	Olinga feredayi	17	8.3
Hydroptilidae	*Oxythira albiceps*	36	17.6
O. Diptera	genus undet.		
Tipulidae	"	1	0.5
Chironomidae	"	7	3.4
Empididae	"	3	1.5
Ceratopogonidae	"	3	1.5
O. Coleoptera			
Elmidae	"	1	0.5

N* = number of birds in which food item was found

%* = percentage occurrence

known to feed on freshly ploughed ground (Mr Bill Gray, pers.comm.). Mr Gray believed that these birds were eating earthworms.

ii) *Plant material*. Plant food, primarily foliage, was clearly the main food of the Paradise Shelducks (Table 2). Both vegetative and seed material of a number of plant species were present in the shelducks examined. For the purposes of this analysis, it was convenient (and in some cases necessary) to group various species. For example, species of *Trifolium* and *Medicago* are referred to collectively as clovers; grasses are included as a single category and the vegetative parts of rushes and sedges are considered as a group.

Terrestrial Plants. Vegetative parts of terrestrial plants predominated in the shelduck's diet. Foliage of clover and grass occurred in a far greater proportion of the shelducks than did any other food item. Of the two, clover was the preferred food. This was shown by both the percentage occurrence (Table 2), and also by the relative quantities present in each bird. Where mixtures occurred - as in most cases - 80% or more of the bulk was generally clover. Several of the plant species classified here as "terrestrial" are nevertheless often found growing in shallow water or near its edge. The leaves of rushes and sedges for instance formed quite an important part of the shelduck's diet. This was the only other category of terrestrial vegetative material which occurred in over 20% of the birds. A soft-leafed rush, *Juncus articulatus*, is common in the study area, and this appeared to be the major rush species eaten.

Leaves of two herbaceous species, *Rumex acetosella* and *Taraxacum officinale*, both of which are common in permanent pasture and on riverflats in the study area, were each encountered in 14 of the shelducks examined. Immature flower buds of *Hypochaeris* sp., which was also common in the study area, were taken, although leaf material of this species was not. Leaves of every other terrestrial plant species ingested were recovered from less than 5% of the shelducks.

Seeds of several species were commonly present, usually within the gizzard. Most seeds resist breakdown for much longer than other items eaten by shelducks, and some eventually pass out with the faeces, still viable. It is recognised that their longer breakdown time must cause an over-estimate of the occurrence of hard gizzard grit sized seeds, but without feeding experiments with captive shelducks a correction factor cannot be calculated. Interpretation of occurrence percentages must therefore be made with care. This is thought to be of particular importance in the case of *Scirpus* "nuts", which were present in 23% of the birds. These are particularly hard shelled, and as they are of a very similar size to gizzard grit they are probably retained for some time after ingestion.

Except for those of oats, terrestrial plant seeds which were eaten intentionally appeared to have been taken by the shelducks in two main forms - as seed heads and as berries.

Seeds of all the monocotyledonous species were probably ingested simply by plucking at the seed heads. Nearly complete seed heads of grasses were found in several of the shelducks, and material which appeared to be the stalk portions of seed heads were nearly always found when *Juncus* seeds were present. Similar evidence was not found with sedge seeds, but nevertheless, the same technique was almost certainly used to obtain these.

Some of the clover seeds were probably also taken in as seed heads. It does not appear that they were strongly selected for as no birds contained very large numbers of these seeds. The most commonly found clover seed was that of *T. subterraneum*. Unlike those of the other species of clover present, the seeds of *T. subterraneum* are not contained in aerial flower heads. Because the calyx of this species is borne so close to the stem of the plant, the seeds are more susceptible to being eaten along with vegetative parts of the plant.

"Berries"[1] appear to form an important part of the diet of many of the shelducks. Those of *Muehlenbeckia axilaris* in particular were eaten very frequently, and those of *Gunnera dentata* and *Cyathodes fraseri* were often taken. Generally, only the seeds from "berries" of these species remained in the tracts. Seeds from the "berries" of other species were also found but they occurred infrequently and were usually sparse.

Where shelducks have access to them, oats, *Avena sativa,* take over as the most important part of the diet. Eleven of the birds examined contained oats or oat husks. In some cases these may have been obtained from stubble fields, but in most cases the grain had been spread by farmers to supplement the winter diet of their sheep. The shelducks are quick to utilise this source of food.

Aquatic Plants. Filamentous algae was the most commonly eaten aquatic plant and was the only type which occurred in the tracts of over 20% of the shelducks. *Drepanocladus* sp., an aquatic moss, was the next most common but occurred in only 10 birds. *Ranunculus fluitans* was found in seven. *Lemna minor* and *Elodea* sp. were rarely present. Although no leaves of *Potamogeton* sp. were found, seeds were present in several of the birds.

b) Seasonal Variations in Diet - The flocking of Paradise Shelducks has already been discussed in a previous section. Almost all shelducks collected from the study area in May 1972 were "flock-birds" which had been shot over cultivated pasture. They had almost without exception been eating clover and/or grass. However, birds taken after May 1972 under special permit were almost all taken on undeveloped land on riverflats or low terraces of the rivers in the study area. Thus an apparent abrupt change in diet seen between the May and June 1972 samples, reflects to a large extent a

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1 NB. For convenience the term "berries" is used to cover all fleshy fruits and those fruits surrounded by a fleshy layer, regardless of the origin of this layer.

Table 3. SEASONAL VARIATION IN DIET COMPONENTS.

Incidence* of Diet Components in Monthly Samples

Month	Terrestrial vegetative material	Sedge and rush seed	Clover seeds	Grass seeds	"Berries"	*Hypochaeris* flower buds	Oats	Terrestrial and free-flying animal material	Aquatic plant material	Aquatic animal material
MAY	10	3	-	-	1	-	-	-	1	-
JUNE	6	5	-	-	-	-	-	1	9	6
JULY	6	3	2	1	-	-	3	-	8	5
AUGUST	7	6	4	-	-	-	-	3	8	5
SEPTEMBER	10	2	-	-	-	-	-	4	2	2
OCTOBER	9	2	-	-	-	-	-	-	3	4
NOVEMBER	7	-	-	3	10	2	-	1	1	2
DECEMBER	8	3	-	3	6	2	-	1	5	5
JANUARY	6	1	1	2	5	3	-	3	1	2
FEBRUARY	5	4	-	-	9	4	-	5	6	7
MARCH	6	2	3	-	5	2	1	1	5	6
MAY	10	5	4	1	3	1	3	-	3	1

* "Incidence" refers to the number of ducks in each monthly sample of ten, which contained a particular food item.

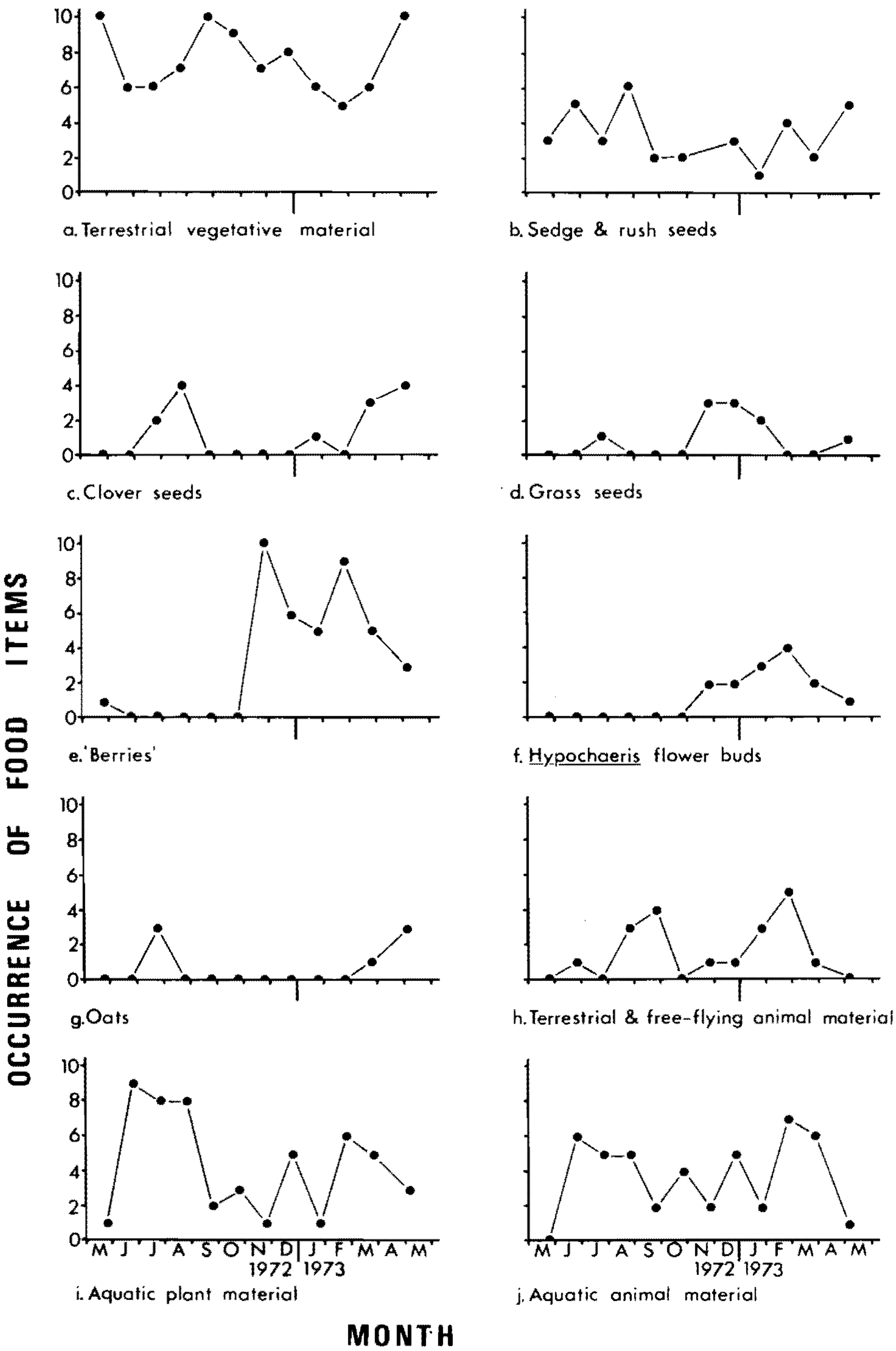


Figure 8. Seasonal variation in diet components.

shortcoming of the sampling method. To a smaller extent a real change may be due to the shelducks moving away from the cultivated areas after disturbance during the shooting season.

Table 3 presents the occurrence of food items in each monthly sample of 10 birds. Care must be taken when extrapolating from such small samples. Many of the fluctuations present almost certainly do not represent similar changes in the population as a whole. Nevertheless, some obvious seasonal variations in diet are revealed.

i) *Terrestrial vegetative material* (Fig. 8a). No marked seasonal pattern stands out. Vegetative material - particularly clover, grass and rush - is an important part of the diet throughout the year. It is probably most important during autumn when the birds are mobbing, and winter when little other food is available. An apparently slight fall off in its importance from spring through to autumn may be due to the availability of a greater variety of food during these seasons.

ii) *Sedge and Rush seeds* (Fig. 8b). Again there is no marked seasonal pattern, but the occurrence gradually drops from late winter until the following autumn. This may reflect the availability of these items. Ripe seedheads - of sedge in particular - may be retained on the parent plants throughout the winter. The slow rate of breakdown of sedge seeds after ingestion may be partly responsible for their apparently extended period of occurrence.

iii) *Cloverand Grass seeds* (Fig. 8c & d). Grass seedheads were usually eaten before they had ripened. They occurred most commonly between November and January. Whole stems of Suckling Clover (*T. dubium*), including flowerheads, were present in some of the shelducks in November, but throughout most of the year, cloverseeds of all species appeared to have been ingested after they had matured. The seasonal pattern of occurrence simply reflects the availability of this material.

iv) *"Berries"* (Fig. 8c). The most noticeable seasonal influence on the diet of the shelduck is the presence of "berries". When "berries" become available they appear to be a much favoured food. Those of *Muehlenbeckia axilaris* are particularly important, but those of *Cyathodes fraseri* and *Gunnera dentata* are also eaten frequently. *Muehlenbeckia* seeds and fruit first appeared in the shelducks in November while those of *Cyathodes* appeared in December and those of *Gunnera* in February.

v) *Hypochaeris Flower Buds* (Fig. 8f). These are considered as a separate entity because they often appeared to be selected for separately from the vegetative parts of *Hypochaeris*. They were commonly found as part of the diet between November and April. They show a similarly seasonal pattern of occurrence to "berries".

vi) *Oats* (Fig. 8g). These are utilised when available and can become an important source of food in winter for some birds.

vii) *Terrestrial and Free-flying Animal Material* (Fig. 8h). Because *Dorylaimus* are taken in incidentally with plant material their presence depends on two factors - their abundance and the amount of plant material eaten by the shelducks. The first peak in Fig. 8h is due entirely to the presence of *Dorylaimus* and may reflect to some extent the amount of plant material eaten. The second peak in this graph on the other hand appears to correspond with the flying time of many aquatic insects. These species form the bulk of the insects which brought about this peak.

viii) *Aquatic Plant Material* (Fig. 8i). Aquatic material is commonly eaten throughout the year. To some extent its importance in the diet may depend on the availability of terrestrial plant food. Due to fluctuations in data from small samples any seasonal trends are difficult to see, but apparently it is favoured least in spring and summer. This may correspond to the availability of berries. It is important to recognise that broods of young shelducks are restricted in their mobility and this in turn restricts the parent's ranging as well. Thus the types of food eaten by shelducks during the breeding season depend greatly on local availability of various food species.

ix) *Aquatic Animal Material* (Fig. 8j). The presence of this material depends to a great extent on the presence of aquatic plant material. A comparison of Fig. 8i and 8j reveals the similarity of their monthly pattern.

VII. DISCUSSION AND CONCLUSIONS

Seven species of shelducks are known throughout the world, one of which may now be extinct. Although Delacour (1963) united all seven into the single genus *Tadorna*, he recognised that four - *T. tadornoides*, *T. variegata*, *T. cana* and *T. ferruginea* - fall into a natural group, which he believed were better considered a superspecies. He referred to the members of this group as the "Casarcas". They are all basically similar in appearance, behaviour and ecology, but differ considerably from the other species of the genus - *T. tadorna* and *T. radjah*. The biology of the Korean Crested Shelduck *T. cristata*, is apparently unknown, and the species is possibly extinct (Delacour, 1963).

The ecology of the Casarca group resembles that of geese more than that of other shelduck species. McAllum (1965) noted that the goose-like trait of grazing exhibited by Paradise Shelducks is most evident when large flocks congregate after moulting. He mentions damage to pasture caused by this behaviour. The results obtained in the present study verify that pasture plants are of prime importance to flock birds in autumn (although when birds have access to grain, grazing becomes of secondary importance, Bisset, 1971). However, it is evident that other types of food, particularly leaves of rush, filamentous algae and berries in season are of considerable important to the Paradise Shelduck at other times of the year.

The Australian Shelduck *T. tadornoides* has very similar feeding habits to the New Zealand species. Frith

(1969) said that the diet of the Australian species consists mainly of the seeds and leaves of clover, green algae, some duckweed and pondweed, and small amounts of herbs characteristic of the water's edge. He added that insects are found in 40% of the birds but that these contribute little to the bulk of the food. Similarly, the South African Shelduck *T. cana* and the Ruddy Shelduck, *T. ferruginea* of Asia and Europe, are birds of inland freshwaters and are omnivorous, but eat mainly plant material.

On the other hand, Delacour described the diets of *T. tadorna* and *T. radjah* as primarily consisting of worms, crustaceans and molluscs. Olney (1965) has shown that *T. tadorna* wintering on the Thames Estuary, eat almost exclusively the small estuarine snail *Hydrobia ulvae*. However, Hori (1969) found that during the laying and incubation periods the breeding adult birds mainly graze on freshwater marshes. The non-breeding birds continued to feed on the intertidal zone.

Although animal material is an unimportant part of most Paradise Shelducks diets, no birds under one month old were examined in this study. Thus, the extent to which animal material is utilised by very young shelducklings is unknown. Two one-month-old ducklings contained mainly *Muehlenbeckia* "berries", with grass leaves and seed-heads, suckling clover, and *Hypochaeris* flower-buds making up most of the remainder of the bulk. Although one contained several *Dorylaimus* sp., neither contained animal material of nutritional importance. Thus, the diet of ducklings at one month old appears to be very similar to that of the adult birds. Because they probably require a fairly protein-rich diet, young ducklings of less than one month may depend much more on animal material for their nutrition than the food remains found in the older ducks would indicate.

CHAPTER IV

COMPOSITION AND DISTRIBUTION OF THE HELMINTH FAUNA

I. INTRODUCTION AND METHODS

The endoparasite fauna of the Paradise Shelduck *T. variegata* was poorly known. Thus, a major aim of this study was to identify the intestinal helminths present, and to find their usual locations within this host.

Parasites were removed from the gastrointestinal tracts as soon as possible after the birds had been shot. Freezing or preservative was not normally used, as mature parasites in fresh condition were required for life history investigations. Each monthly sample of 10 shelducks was refrigerated without freezing while examination of each bird in that sample was completed. However, in May 1972, when the sample was too large to be dealt with without deterioration taking place, freezing of part of the sample was necessary.

Extraction of parasites began by initially washing the exterior of the whole gut over a fine mesh sieve (Mesh No. 72; aperture 210 microns). This was necessary as sometimes shotgun pellets perforated the gut and released helminths to the outside. The washings were inspected for helminths. The gut was then divided up into discrete regions, *viz.* the oesophagus, proventriculus, gizzard, "small intestine 1" (consisted of the duodenum and jejunum), "small intestine 2" (ileum), caeca, large intestine, cloaca and bursa of Fabricius (see Fig. 9). Each of these sections was split longitudinally with a pair of scissors and the contents washed into the sieve with flowing water. The walls of each section were inspected as they were washed to ensure that they were free of helminths that may have remained adhering to the mucosa. Finely divided material and mucus were then washed through the sieve and the remaining material inspected for parasites under a stereoscopic dissecting microscope.

The oesophagus, proventriculus and gizzard of birds collected in May 1971, were not investigated for the

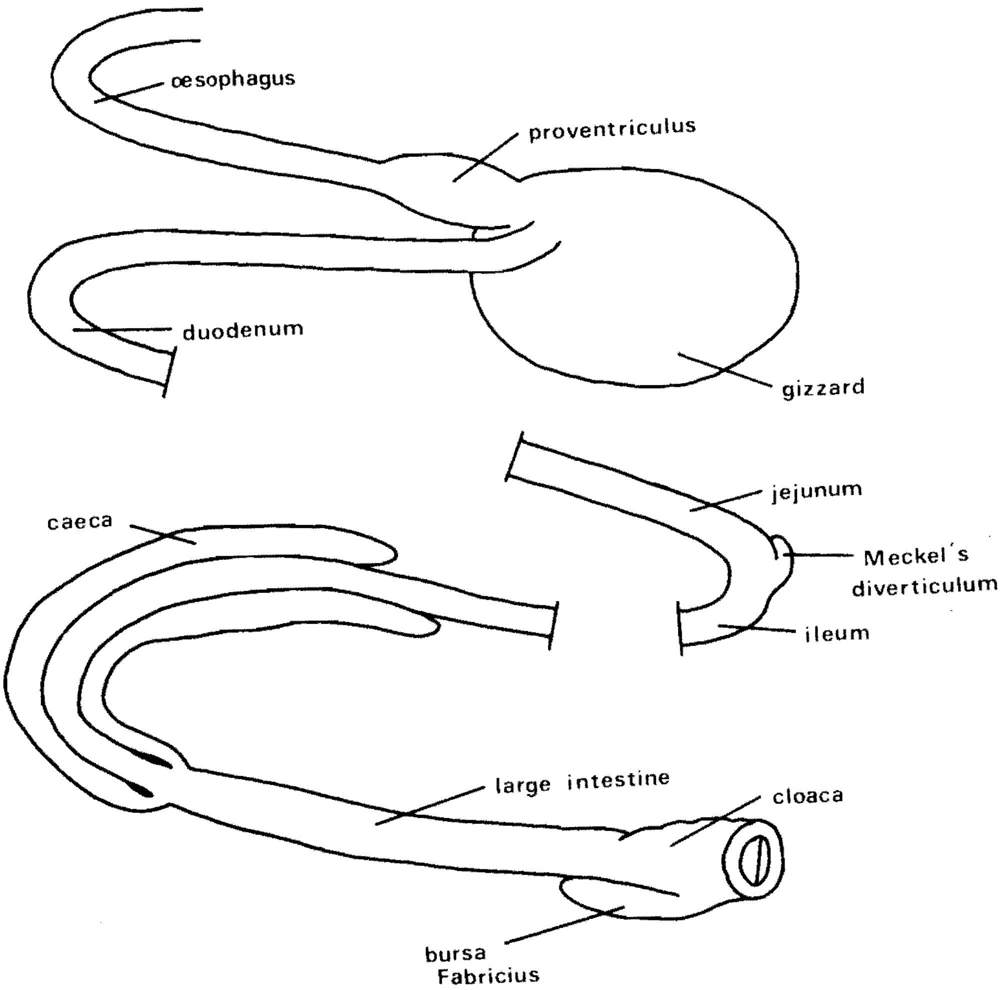


Figure 9. Diagrammatic representation of the gut of a Paradise Shelduck showing the major regions.

presence of parasites, but these regions were examined in subsequent samples.

Platyhelminths were counted and placed in 70% ethanol unless they were required for life history investigations or the preparation of slides. If this was the case, they were placed in a warm saline solution until required. All nematodes were preserved immediately in 70% ethanol as no life history studies were made for nematodes, and satisfactory whole mounts could be prepared from specimens treated in this way.

Trematodes and cestodes required for the preparation of slides were usually held flat under a coverslip and fixed in Bouin's fixative. They were then stained in either Delafield's haematoxylin or acetocarmine and mounted in Xam. A small number of specimens were mounted directly in Lactophenol P.V.A. with lignin pink. The haematoxylin was the most successful method of staining in most cases, but for identification of the various species of notocotylid this proved inadequate. The arrangement of ventral glands, which is important for specific identification of the notocotylids, was often not visible in stained and mounted specimens. It was necessary to manipulate unmounted specimens of each species into a suitable position for viewing under a stereoscopic microscope to observe the arrangement and numbers of these structures. The ventral glands were most easily observed on live specimens. A scanning electron microscope was used successfully for obtaining photographs of the ventral glands of these species.

With experience it was possible to recognise the different notocotylid species simply from their general appearance, although a random sample from each infection was always taken to check gland arrangement.

With the exception of one very large species, nematodes were transferred from 70% ethanol in which they were stored, to a 5% solution of glycerine in 70% ethanol. The 70% ethanol was then evaporated off in a drying oven at 50°C and the cleared nematodes mounted in glycerine jelly (method recommended in Carlton and Drury, 1957). This technique was found to be quite satisfactory for the smaller species of nematodes, but it was not suitable for clearing *Porrocaecum crassum* because of its large size. Lactophenol P.V.A. and creosote were suitable as clearing agents, but both caused severe shrinkage after a short time. Dissection was found to be the most successful method of investigating the gut structures of this species. Gut structure is important in generic classification of members of this family (Baylis, 1928).

II. HELMINTHS RECOVERED FROM THE PARADISE SHELDUCK *T. VARIEGATA*

A number of authors were consulted for the identification of helminths found during the study. Of these Beverley-Burton (1958, 1961, 1964), Bezubik (1956), Cram (1927), Dubois (1968), Madsen (1945), McDonald (1974), Yamaguti (1958, 1959, 1961) and Yorke & Maplestone (1962) were the most important.

A total of 22 helminth species was found in the material studied. Five species of cestode, eight species of trematode and six species of nematode were recovered from the alimentary tracts of the shelducks. Two other species of trematodes were found, one inhabiting the trachea and the other the blood vessels in the liver region. In addition a single unidentified nematode was found but its habitat is uncertain.

Few of the helminth species infecting waterfowl are confined to only one species of host, and most have been found in several. All species of cestodes and nematodes recovered from *T. variegata* have been described previously (though from different host species). One species of notocotylid trematode is new.

1) Classification of helminths recovered

The species of helminth parasites recovered from *T. variegata* are listed below:

CLASS CESTODA

Order Cyclophyllidea Braun, 1900

Family Hymenolepididae Fuhrmann, 1907

Subfamily Hymenolepidinae Perrier, 1897

Aploparaksis furcigera (Nitzch in Rudolphi, 1819) Fuhrmann, 1908

Cloacotaenia megalops (Nitzch in Creplin, 1829) Wolffhugel, 1938

Sobolevicanthus gracilis (Zeder, 1803) Spaskii & Spasskaia, 1954

Subfamily Fimbriariinae Wolffhugel, 1900

Fimbriaria fasciolaris (Pallas, 1781) Wolffhugel, 1900

Family Dilepididae Fuhrmann, 1907

Anomotaenia ciliata Fuhrmann 1913

CLASS TREMATODA

Order Digenea

Family Strigeidae Raillet, 1919

Cotylurus cornutus (Rud., 1808)

Family Echinostomatidae Looss, 1902

Echinostoma revolutum (Frolich, 1802) Looss, 1899

Echinoparyphium recurvatum (von Linstow, 1873) Luhe, 1909

Echinostoma sp.

Hypoderaeum conoideum (Bloch, 1789) Dietz, 1909

Family Notocotylidae Lühe, 1909

Notocotylus attenuatus (Rudolphi, 1809) Kossack, 1911

Notocotylus tadornae n.sp. (description Chapter 5)

Uniserialis gippyensis Beverley-Burton, 1958

Family Cyclocoelidae Kossack, 1911

Typhlocoelum cucumerinum? (Rudolphi, 1809) Stossich, 1902

Family Schistosomidae Looss 1899

Dendritobilharzia pulverulenta (Braun, 1901) Skrjabin, 1924

CLASS NEMATODA

Order Eunematoda

Family Trichuridae Raillet, 1915

Capillaria anatis (Shrank, 1790)

Family Trichostrongylidae Leiper, 1912

Amidostomum acutum (Lundahl, 1848) Seurat, 1918

Epomidiostomum uncinatum (Lundahl, 1848) Seurat, 1918

Trichostrongylus tenuis (Mehlis, 1848) Raillet & Henry, 1909

Family Tetrameridae Travossos, 1914

Tetrameres sp.

Family Syngamidae Leiper, 1912? gen. undet.

Superfamily Ascaroidea Raillet & Henry, 1915

Family Heterochelidae Raillet & Henry, 1915

Porrocaecum crassum (Deslongchamps, 1824)

2) Discussion

Of the 22 helminth species recovered from the Paradise Shelduck during the present study, all are new host records except *Uniserialis gippyensis*, *Echinoparyphium recurvatum* and *Echinostoma revolutum*. Rind (1974) reported the recovery of these three species from *T. variegata*.

The helminth fauna found shows a strong resemblance to those found in helminthological surveys of different waterfowl species in the Northern Hemisphere, but the variety of species in the present study is somewhat smaller.

Cestodes - At least three of the cestode species from the Paradise Shelduck - *Aploparaksis furcigera*, *Cloacotaenia megalops* and *Fimbriaria fasciolaris* have world-wide distributions and are well known from many species of waterfowl (McDonald, 1969). *Anomotaenia ciliata* has commonly been reported from Europe and Asia (Bezubik, 1956 and others), and also from North America (Buscher, 1965), but never before from the Southern Hemisphere.

There has been some confusion in the past over the differences between *Sobolevicanthus gracilis* and *Hymenolepis collaris* (Beverley-Burton, 1964). The species found from the Paradise Shelduck is identical to specimens described as *H. collaris* from Australia (Johnston, 1912) and from Poland (Bezubik, 1956). However, Beverley-Burton compared the morphological characters of *H. collaris* and *S. gracilis* and from her descriptions of the proglottids of these two species, it appears that the cestode found in the present study and those described by both Johnston and Bezubik are in fact *S. gracilis*.

Trematodes - Most of the trematode species found from the Paradise Shelduck are also more or less cosmopolitan in distribution.

Only two notocotylid trematodes *Notocotylus tadornae* and *Uniserialis gippyensis* appear to have a restricted distribution. *Notocotylus tadornae* n.sp. has not been reported from any other part of the world, while *U. gippyensis* has been found previously only at Nacton Decoy, England. Taxonomic problems within the family Notocotylidae, and discussion of the biogeography of *N. tadornae* and *U. gippyensis,* are covered at length in Chapter V.

Nematodes - All nematodes recovered from Paradise Shelducks during the study are characteristic of waterfowl species of the Northern Hemisphere. Although they are little known in the Southern Hemisphere, this would appear to be due basically to the lack of work on waterfowl parasites.

The biggest differences between the helminth fauna of *T. variegata* and those of other waterfowl species surveyed elsewhere seems to be the relatively small variety of cestode species present. Beverley-Burton (1972) recorded at least 18 cestode species from 54 Mallards in England, while Bezubik (1956) working in Poland recorded 11 species from 158 Mallards. Kinsella and Forrester (1972) found only seven cestode species from 78 Florida Ducks *Anas platyrhynchos fulvigula* - a race of Mallard - in North America. On the other hand, only two species of cestodes - *C. megalops* and *F. fasciolaris* - normally parasitise the Paradise Shelduck in Canterbury, while a total of only five species were recovered throughout the entire study from the 281 birds examined.

Acanthocephalan species were not present in the Paradise Shelducks from the study area. Acanthocephalans are known to be present in waterfowl in New Zealand, but these are mainly found in hosts collected from estuarine conditions (Rind, 1974). Although no Paradise Shelducks from estuarine habitats were examined during this study, it is considered likely that shelducks which have been feeding in such areas are sometimes infected by acanthocephalans.

Despite the poor variety of cestode species and lack of acanthocephalans, a greater variety of nematodes were found in the Paradise Shelduck than were found by either Beverley-Burton or Bezubik during their studies. However, Kinsella and Forrester (1972) found an even greater number of nematode species (12) infecting the Florida Duck.

III. DISTRIBUTION OF HELMINTHS WITHIN THE GUT

Each region of a host's alimentary tract provides an environment with a specific set of morphological and physiological conditions. Crompton (1973) presented evidence of such variations between regions, and discussed the hypothesis that distribution of helminths in the alimentary tract is related to the different conditions therein.

The consistently similar distribution of helminth species throughout the gut of each Paradise Shelduck indicates the importance of these conditions to the helminth community of each region.

The upper parts of the tract (i.e. oesophagus, proventriculus and gizzard) in most waterfowl species are characteristically inhabited by tissue feeding nematodes (Cornwall and Cowan, 1963). In the regions above the gizzard the host's food has been neither ground nor sufficiently digested for most helminths to utilise it as a source of nutrients. Species parasitic here generally obtain their requirements from the walls of the tract. Within the gizzard parasites normally must live under the koilin lining to escape the pulverising action of this organ.

Helminth species permanently inhabiting the upper tracts of the Paradise Shelducks were all nematodes. The oesophagus of a total of 190 birds was examined during the period between May 1972 and May 1973, but none was infected by helminths.

Similarly the proventriculus is sparsely inhabited. This organ was infected in only one shelduck (collected in November). The helminth present was a nematode *Tetrameres* sp. A single individual was found embedded in one of the secretory glands of the proventriculus wall. Six *Echinoparyphium recurvatum* found in the proventriculus of one shelduck probably reached this region after the host's death - possibly by antiperistalsis. This view is supported by their presence in the gizzard of the same bird.

The gizzard was more commonly inhabited by parasites. The nematode species *Amidostomum acutum* and *Epomidiostomum uncinatum* (usually found under the koilin lining of the gizzard) were often present.

Although the koilin lining was often removed and inspected, no quantitative data were taken for the sample as a whole due to difficulties in separating the lining from the gizzards of many of the birds. However, in several cases these species were also found in the lumen of the gizzard. It is probable that they moved into the lumen after the death of the host, because it is unlikely that they could have withstood the abrasion by the gizzard grit while the host was still living. Neither *A. acutum* nor *E. uncinatum* were found outside the gizzard. In addition to the normal residents, a few individuals of other species - *Echinoparyphium recurvatum, Fimbriaria fasciolaris* and *Capillaria anatis* - were also found in the gizzard. However, it is doubtful that these were residing in the gizzard at the time of death of the host. It is thought that they were probably forced there as a result of antiperistalsis.

The lower regions of the gastrointestinal tracts of waterfowl contain finely divided food material on which digestive processes act strongly. The contents of the gut are consequently rich in available nutrients. Helminths of the lower regions of the tracts of waterfowl are characteristically cestodes and trematodes, though to a lesser extent nematodes are represented here also. Tables 4 and 5 contain the quantitative data relevant to the remainder of the section.

Table 4. UTILISATION OF REGIONS OF THE LOWER TRACT OF 281 SHELDUCKS BY THE MAJOR GROUPS OF HELMINTHS, AS INDICATED BY POST-MORTEM DISTRIBUTION

	Percentage infection					
	"small intestine 1"	"small intestine 2"	caeca	large intest.	cloaca	bursa
Cestodes	40.6	2.1	0.7	1.1	61.2	0.0
Trematodes	34.9	5.0	65.1	11.0	11.7	72.8
Nematodes	9.6	1.8	43.1	1.4	0.4	0.0
Total helminths	62.3	8.5	73.3	11.4	68.7	72.8

The helminth communities occupying the various regions of the lower tract in Paradise Shelducks are as follows:

a) "Small intestine 1" - *F. fasciolaris, E. recurvatum* and *Cotylurus cornutus* were the commonest species found inhabiting this region of the small intestine (Table 5), and they were virtually restricted to this region. *Anomotaenia ciliata* and *Sobolevicanthus gracilis* were rare in the Paradise Shelducks, but when present they were invariably found here. Other species were not as restricted to this region. *Porrocaecum crassum* and *Hypodereum conoideum* were found throughout the small intestine but were more common anterior to the Meckel's diverticulum, while *Echinostoma revolutum* appeared to be the least restricted of all the helminths in locality and was found at similar frequencies in all the regions of the lower tract except the bursa. Although *N. tadornae* was found in the anterior region of the small intestine in seven of the 281 shelducks, the number in this region represents only an extremely small proportion (0.09%) of the total number found. Similarly, the anterior small intestine is not a favoured region for *Capillaria anatis*.

b) "Small intestine 2" - The small intestine widens posterior to the Meckel's diverticulum and the contents within the lumen are different in appearance from those of the anterior region. Posterior to the diverticulum the

Table 5. POST-MORTEM DISTRIBUTION OF HELMINTH SPECIES IN THE GUT OF 281 *T. VARIEGATA*

	oesophagus		proven-triculus		gizzard		"small intestine 1"		"small intestine 2"		caeca		large intestine		cloaca		bursa	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
TOTAL CESTODES					5	0.38	6.21	47.01	8	0.61	3	0.23	14	1.06	670	50.72		
C. megalops													1	0.15	670	99.85		
F. fasciolaris					5	0.81	6.08	97.91	8	1.29								
A. furcigera											3	18.75	13	81.25				
A. ciliata							12	100.00										
S. gracilis							1	100.00										
TOTAL TREMATODES			6	0.04	11	0.07	1141	6.79	40	0.24	14889	88.59	69	0.41	111	0.66	539	3.21
U. gippyensis															100	15.65	539	84.35
N. tadornae							13	0.09	9	0.06	14662	99.46	55	0.37	3	0.02		
N. attenuatus											218	99.09	2	0.91				
E. revolutum							7	23.33	7	23.33	7	23.33	6	20.00	3	10.00		
Echinostoma sp.													3	75.00	1	25.00		
H. conoideum							38	65.52	20	34.48								
E. recurvatum			6	0.61	11	1.11	962	97.17	2	0.20	2	0.20	3	0.30	4	0.40		
C. cornutus							121	98.37	2	1.63								
TOTAL NEMATODES			1	0.11	135	15.41	107	12.22	76	8.68	552	63.01	4	0.46	1	0.11		
C. anatis					1	0.14	75	10.73	72	10.30	546	78.11	4	0.57	1	0.14		
T. tenuis							1	14.29			6	85.71						
A. acutum					105	100.00												
E. uncinatum					29	100.00												
P. crassum							31	88.57	4	11.43								
Tetrameres sp.			1	100.00														

n = number present; % = percentage of total number found contents are coarse and fibrous as compared to the material anterior to this structure. This part of the small intestine has quite a different degree of helminth infection although the fauna appeared to consist of basically the same species. Scolices of *F. fasciolaris* were rarely present, although sometimes the tape of larger specimens did extend past the diverticulum into this region. The region was infected by only small numbers of *E. recurvatum* and *C. cornutus*, but 23.3% of *E. revolutum* were found here. *Notocotylus tadornae* was recorded in the posterior region of the small intestine on three occasions and *C. anatis* on five occasions, but in general the numbers of each were very low. A small proportion of *P. crassum* and *H. conoideum* were also here.

Infection rates for the "small intestine 1" and "small intestine 2" regions indicate the extent of the difference in worm burden. The "small intestine I" region of 62.3% of the shelducks was infected with at least one helminth species, while only 8.5% were infected in the "small intestine 2" region (Table 4). Cestodes were the most common group parasitising "small intestine 1", followed by trematodes and nematodes, while trematodes were the most common in "small intestine 2", followed by cestodes and nematodes.

Cornwall and Cowan (1963) studying the Canvasback Duck (*Aythya valisinera*) found that the small intestine was the most often infected area of the lower alimentary tract with an overall infection rate of 96%. However, this does not appear to be the case for the Paradise Shelduck. For the total sample of shelducks the number of small intestines infected with some species of helminth was 171 (or 63.3%). This means that the small intestine is only the fourth most frequently infected region of the lower alimentary tract despite the fact that a wider variety of helminths live there than in any of the other regions of the tract.

c) Caeca - These are blind ending branches of the gut arising from the junction of the ileum and the large intestine.

Their function is unknown although some workers suspect they may be involved in either water retention (Bradley, 1950) or cellulose breakdown (Marriot and Forbes, 1970). They are relatively large in the Paradise Shelduck (approximately 100-150 mm in length), and in general they are found to contain food material so finely divided as to be paste-like. The caeca are evacuated by periodic contractions.

The basic helminth fauna of the caeca is made up of only two common species - *N. tadornae* and *C. anatis*. *Echinostoma revolutum* was also sometimes present in this region and infections by *N. attenuatus* were generally located here. In only one bird was there a mixed infection of *N. tadornae* and *N. attenuatus*. Its caeca contained three *N. attenuatus* and 60 *N. tadornae*. Four other species - *Aploparaksis furcigera, Trichostrongylus tenuis, Echinostoma revolutum* and *Echinoparyphium recurvatum* - were all occasionally found in the caeca. *Aploparaksis furcigera* was the only cestode found in this region. From my observations of Mallard and Grey Ducks (in which *A. furcigera* is a particularly common parasite), it seems that the caeca are a normal part of the habitat of this species, but are not the most favourable region.

The caeca of 73.3% of the shelducks were infected by helminths, making this overall the most commonly parasitised region of the lower alimentary tract. Trematodes, in particular *N. tadornae*, formed by far the largest component of the caecal fauna. The caeca of 61.5% of the shelducks were infected with trematodes, while nematode infections were present in the caeca of 43.1% of the birds. Cestode infections were recorded in the caeca of only 0.7% of the shelducks in the sample.

d) Large intestine - This is a short but very thick-walled and muscular section of the gut. Like the "small intestine 2" region the lumen of the large intestine contains coarse food material and a relatively small number of helminth parasites.

Of the 281 shelducks in the total sample, the large intestine of only 32 were infected with helminths (i.e.

11.4%). Trematodes infected 31 of the large intestines of these birds and were consequently the most abundant group in this region, while nematodes and cestodes infected this region in only four and three birds respectively.

The nematodes and most of the trematodes present in the large intestine were of the same species that were normally found in the caeca (i.e. *N. tadornae, C. anatis,* and *N. attenuatus*). However, because numbers of these species were so low in the large intestine compared to those in the caeca, it is thought that this region would not normally be permanently inhabited by them in live and healthy hosts.

Other trematode species present were *E. revolutum, Echinostoma* sp., and *E. recurvatum*. Only *Echinostoma* sp. appears to be restricted to the region. *Echinoparyphium recurvatum* was found here only twice.

Two cestode species were found in the large intestine during the study. A single specimen of *Cloacotaenia megalops,* a species found very commonly in the cloaca of the Paradise Shelduck, was recovered with its scolex just inside the border of the large intestine and the cloaca. The other cestode *A. furcigera* was most commonly found in this region.

e) Cloaca - The cloaca provides an environment which one might expect to be lacking available nutrients. However, despite this the cloaca is an extensively parasitised region of the gut of *T. variegata* (68.7% were infected by helminths, making this the third most commonly infected region). *Cloacotaenia megalops* is particularly common in the cloaca and it is virtually restricted to this region. As with other regions of the lower alimentary tract, *E. revolutum* was present, but at a relatively low incidence. The only other species regularly recovered from the cloaca was *Uniserialis gippyensis*. One hundred specimens occupied the cloacas of 27 of the shelducks, though this represented only 15.6% of all *U. gippyensis*. Although the species was found here it is thought unlikely that it normally exists as a permanent resident in this region. Other species found in the cloaca were *N. tadornae, Echinostoma* sp., *E. recurvatum* and *C. anatis,* but none of these constitute anything but a minor part of the helminth community of the cloaca, if indeed they were inhabiting the region at the time of death of the hosts.

f) Bursa of Fabricius - The bursa is the second most parasitised organ in the alimentary tract of *T. variegata* (overall 72.8% of bursae were found to be infected). During May the bursa is even more heavily infected than the caeca. At this time of the year 78% of bursae were infected as compared to 72% of caeca. *Uniserialis gippyensis* was the only helminth species found in the bursa throughout the entire study. Note that while a high percentage of bursae were infected, this should not be interpreted as meaning that a similar proportion of the total population of shelducks was infected, as the bursa is a temporary structure only.

It appears that *U. gippyensis*, when in the bursa, feeds on tissue or blood. None of the host's food material was ever found in the bursa. Only mucus was ever present. Individuals of *U. gippyensis* when taken freshly from the bursa were always reddish in colour, probably due to the presence of the host's blood corpuscles in their gut caeca. Stunkard (1967) also noted the presence of blood in the caeca of *U. breviserialis*.

IV. POST-MORTEM MOVEMENTS OF HELMINTHS

Although all species of helminths found in the various regions of the alimentary tracts are given, it is probable, as has been stressed previously, that some of these are not normal or permanent inhabitants of these regions. The extent to which post-mortem movements of parasites played a part in their observed location is uncertain, although the usual site occupied by each species is clear. There are several ways by which parasites could reach unusual positions in the gut:

1) Movement by the parasites themselves as a response to changed conditions after the death of the host - Leland and Drudge (1957) reported post-mortem movements of *Trichostrongylus axei* from the wall to the lumen of the gut of rabbits.

2) Post-mortem antiperistaltic movements of the host's gut.
3) Sometimes, under conditions of overcrowding, parasites may extend their range (Levine, 1938 and Beaver, 1937).
4) Pressure on the gut - both when the bird is shot and falls to the ground and accidental pressure during autopsy.
5) It is inevitable with shot ducks that in some cases gut walls will be pierced. Parasites could move or be carried into other regions by this means.

The trematodes and nematodes are probably more prone to these sorts of movements than cestodes. However, it is believed that in most cases, helminths which were not in the regions they normally occupied, were near or at a junction with that region. For example, *U. gippyensis* was found fairly frequently in the cloaca, although generally the species is found in the bursa of Fabricius. The entrance to the bursa is situated in a pocket-like fold in the wall of the cloaca and it was here that *U. gippyensis* was encountered in many cloacal infections. In the few infections of adult birds by *U. gippyensis* it is likely (but not certain), that this was the part of the cloaca inhabited by the species.

CHAPTER V

LIFE HISTORIES OF THE HELMINTHS RECOVERED

I. INTRODUCTION

Successful transmission from one definitive host to another is a vital part of the biology of any parasitic species. Most helminths, particularly cestodes and trematodes, have life histories involving one or more intermediate host, which enhance the probability of successful transmission. The success of a parasite species in a particular host species, depends on how well its life history ties in with the ecology of that host. The life histories of the helminths of the Paradise Shelduck were investigated to discover this relationship.

Most of the helminth species found in the Paradise Shelduck are widely distributed throughout the world, and so the life cycles of several have been studied previously overseas. However, these studies in general, cannot directly apply in New Zealand because while the cycles are probably basically similar here, many of the intermediate host species utilised elsewhere are not present in New Zealand. No account has been published of the complete life history of any helminth of the indigenous or introduced waterfowl in their New Zealand habitat. Winterbourn (1974) gave a brief account of the larval parasites recovered from the prosobranch snail *Potamopyrgus antipodarum*, and Macfarlane (1949) described a larval schistosome from lymnaeid snails in South Island lakes.

The experimental work undertaken during the present study includes investigations of the life histories of *U. gippyensis, N. tadornae* and *C. megalops*.

II. GENERAL METHODS

An indication of potential intermediate hosts in the study area was needed as a starting point for the life history investigations. A fine mesh net was used to make a collection of aquatic invertebrate fauna from a slow-flowing backwater of the Hope River at a site where shelducks had often been observed.

Four mollusc species were found to be present - *Potamopyrgus antipodarum*, *Gyraulus corinna*, *Physastra variabilis* and the bivalve *Sphaerium novaezelandiae*. Molluscan nomenclature follows Winterbourn (1973). An ostracod species *Herpetocypris pascheri* and a copepod *Cyclops* sp. were the only crustaceans collected.

These species were bred in the laboratory in 21 x 26 cm flat-bottomed sorting trays, and cultures of each of them prepared in 200 ml plastic pots of pond water containing oxygen weed *Elodea canadensis*.

Mature parasites of the species whose life histories were to be investigated were selected and their identity thoroughly checked. Eggs teased from these parasites were placed into the cultures of parasite-free invertebrates. They were kept in a light position at room temperature and observed frequently. Helminth larvae subsequently obtained from the successfully infected intermediate hosts were examined alive and after being killed in warm 10% formalin. The use of neutral red, a vital stain, facilitated the examination of live specimens.

Infective larvae eventually obtained from the cultures were force-fed to incubator-hatched ducklings (generally Pekin-Aylesbury cross), which were killed two to four weeks after infection and inspected for the presence of parasites.

III. DESCRIPTION AND LIFE HISTORY OF *NOTOCOTYLUS TADORNAE* N.SP.

During the study 181 shelducks inspected for parasites were found to be infected with a previously undescribed notocotylid trematode species. Of nearly 15 000 specimens recovered from these birds, 99.5% were recovered from the caeca and the remainder from the small and large intestines.

1) Life History Experiments

Eggs teased from mature specimens of this species were placed in cultures of laboratory-bred molluscs. The species used were *P. antipodarum*, *G. corinna*, *P. variabilis*, *Physa* sp. and *S. novaezelandiae*. Metacercariae were first observed encysting on the walls of the containers of the

P. antipodarum cultures 14-20 weeks after the eggs had been added. Several of the *P. antipodarum* from the cultures were crushed between microscope slides and observed. Most were heavily infected with rediae and cercariae. None of the four other mollusc species cultured was successfully infected.

Metacercariae from the infected cultures were collected on several occasions and force-fed to incubator-hatched two to three day old chickens and ducklings. No successful infections took place in the chickens, but adult parasites were recovered from the caeca of all experimentally infected ducklings. Generally less than half of the metacercariae fed to the ducklings developed into adult parasites - 41 adult notocotylids were recovered from a duckling fed approximately 100 metacercariae, 60 from a duckling fed approximately 200 metacercariae and one from a duckling fed 20 metacercariae. However, on one occasion 14 adults were recovered from the caeca of a duckling fed 20 metacercariae.

Although other areas of the tracts of the experimentally infected ducklings were examined, none of the parasites were ever found outside the caeca. Mature specimens with ripe eggs were not recovered in any infections under 22 days old.

2) Taxonomic Descriptions

The genus *Notocotylus* was extended by Baer and Joyeaux (1961) to include notocotylid species with one, three or five rows of ventral glands. The species described below is typically notocotylid in general body appearance and internal anatomy and has a single median row of ventral glands. It therefore appears to lie in the genus *Notocotylus*.

The following descriptions are based on observations of both live and fixed specimens recovered from both naturally infected shelducks and experimental hosts. Adult worms were fixed in cold Bouin's for one hour while being held flat under slight coverslip pressure. They were stained with either Delafield's haematoxylin or acetocarmine and mounted in Xam mountant. Measurements are based on 30 mature specimens of typical appearance. Transverse sections of some specimens were made and stained with Erlich's haematoxylin, Mallory's triple or Alcian blue, but detail of the ventral glands was disappointing. Several specimens were prepared for examination under a scanning electron microscope. A critical point drier was used to reduce the problems of shrinkage and shape changes of specimens during the drying process of this preparation.

The larval stages were examined by dissecting experimentally infected snails. The use of neutral red, a vital stain, facilitated the examination of live specimens. Because all larval stages are able to vary in size and shape, the most suitable method of obtaining measurements for descriptive purposes was found to be to kill the larvae in warm 10% formalin immediately after they had been removed from their snail hosts. They then tended to be fixed in relatively natural relaxed positions.

FAMILY NOTOCOTYLIDAE LÜHE, 1909

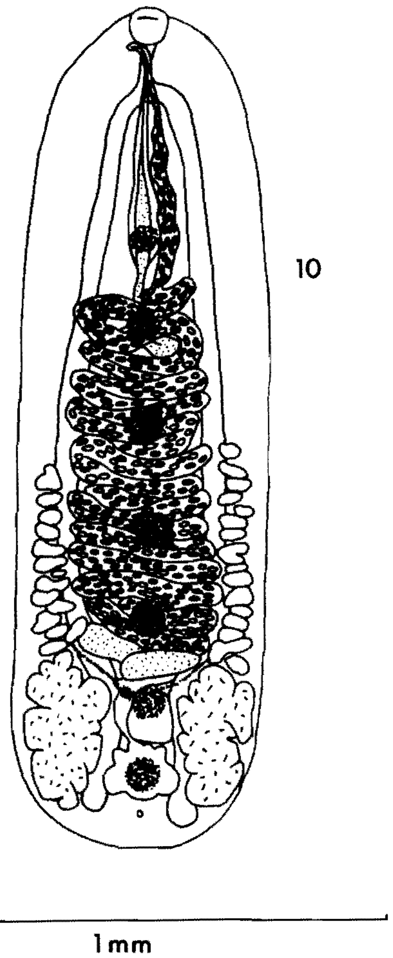
Subfamily Notocotylinae Kossack, 1911

Genus *Notocotylus* Diesing, 1839

Notocotylus tadornae n.sp.

ADULT (Figs 10, 12)

Body dorsoventrally flattened, elongate and more or less parallel-sided with bluntly rounded ends, slightly more attenuate anteriorly than posteriorly. In fixed unmounted specimens, body ventrally concave. Live specimens yellow-brown to red-brown when first recovered from host. Mature specimens 1.46-1.92 mm long, 0.47-0.65 mm wide at anterior extremity of vitellaria. Ventral surface with a single median row of seven ventral glands (occasionally eight) (Fig. 12). Positions of glands relative to internal organs are shown in Fig. 10. Cuticle spinous on ventral surface but is sloughed and lost easily during fixation (Fig. 13). Oral sucker practically terminal 0.070-0.096 mm wide; mouth slightly



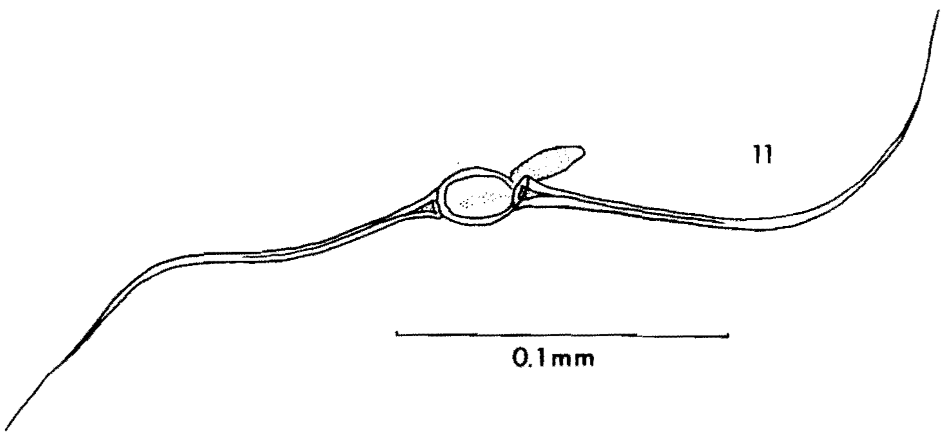
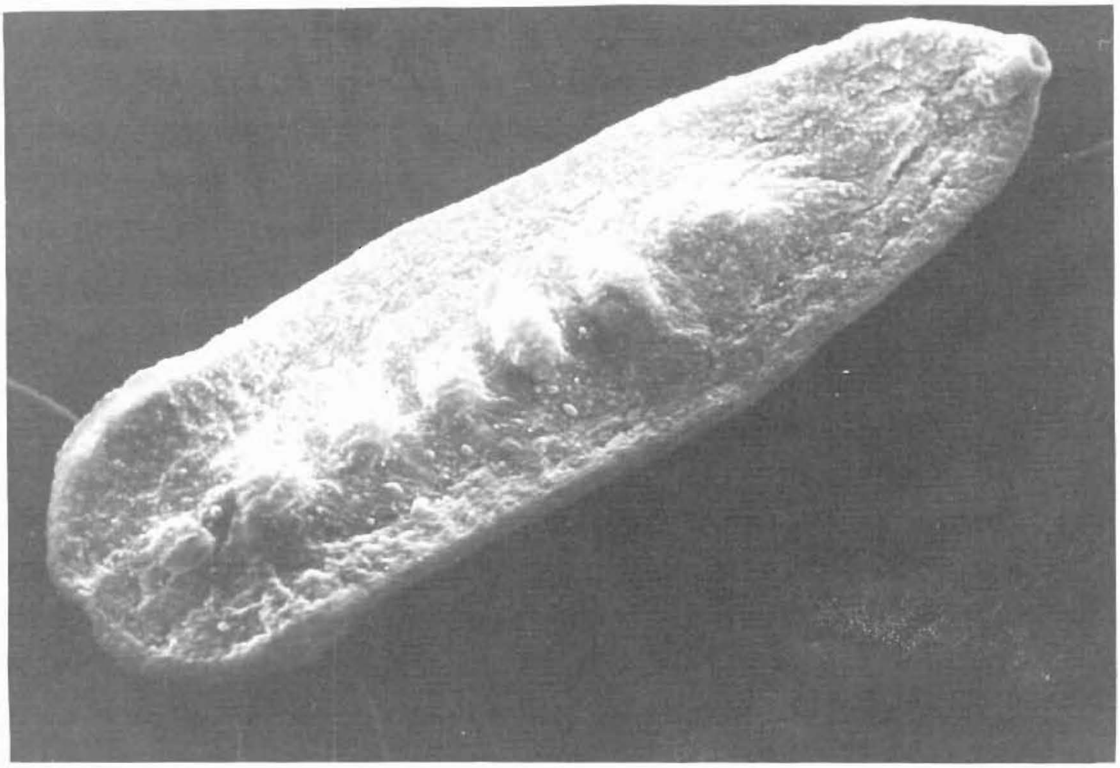


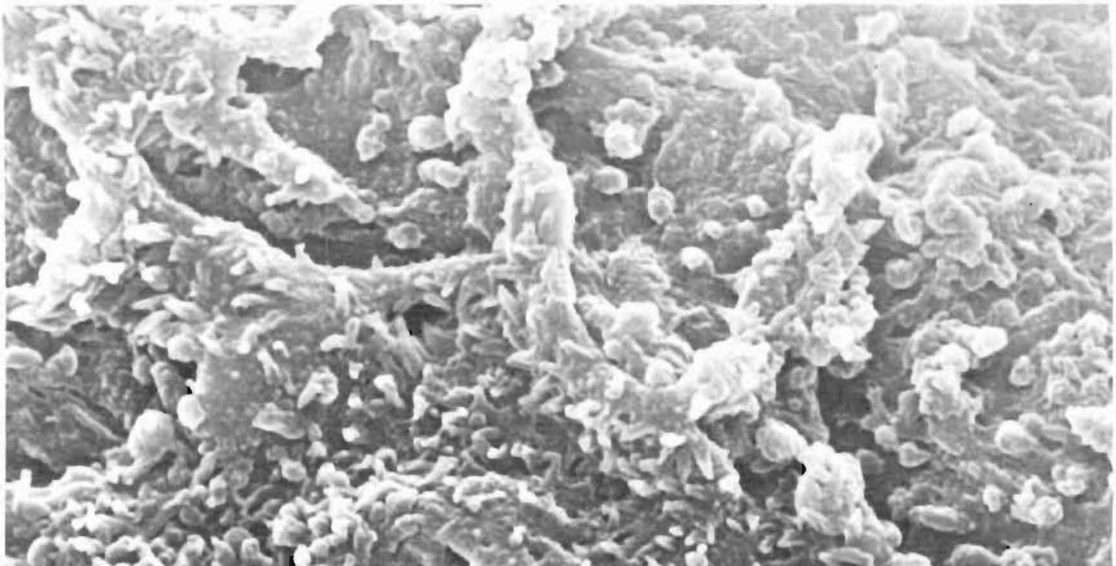
Figure 10. Mature adult specimen of *Notocotylus tadornae* (drawing based on photograph)

Figure 11. Egg of *N. tadornae*. Note opening of the operculum due to pressure from the cover-slip, allowing release of the miracidium. (drawn by camera lucida)

Figure 12. Scanning electron micrograph of *Notocotylus tadornae* n.sp. showing single median row of seven ventral glands.

Figure 13. Close-up of ventral surface of *N. tadornae* showing spinous cuticle. Note sloughing of cuticle.

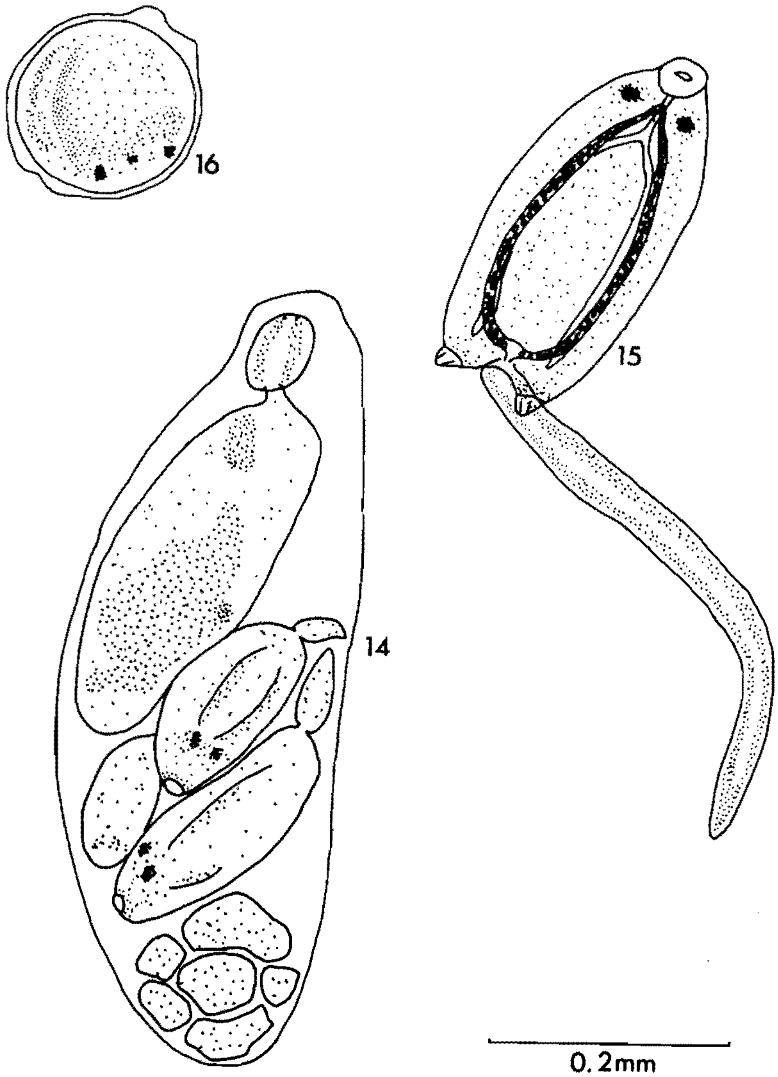




ventral, opening into short oesophagus 0.107-0.167 mm long. Gut caeca smooth to slightly crenulated on outer surfaces, diverging to pass around uterine coils but converging again briefly to pass inside testes and terminating just posterior to them. Testes shallowly lobed and generally uniform in size - 0.24-0.47 mm long by 0.13 mm wide. Vitelline regions extracaecal, lying just anterior to, or sometimes slightly overlapping with testes; extending anteriorly to about midway along body (ratio of body length anterior to vitellaria to total body length 0.42-0.58mm). External seminal vesicle extends posteriorly, dorsal to uterine loops, to join vas deferens midway between the anterior and posterior extremities of uterine region. Anterior portion of external seminal vesicle forms one to three loops before entering cirrus sac. Distance from base of cirrus sac to genital opening 0.31-0.53 mm by 0.041-0.81 mm at widest point. Cirrus unarmed. Ovary 0.10-0.18 mm long by 0.12-0.19 mm wide, weakly lobed; position median intercaecal and between the posterior ends of the testes. Mehlis' gland lies just anterior to the ovary and is 0.10-0.15 mm in diameter. Ducts from the vitellaria meet on its ventral surface. Uterus begins to loop just anterior to the Mehlis' gland and a series of 12-17 transverse loops are formed which are entirely intercaecal. Metraterm extends to about two-thirds the length of the cirrus but is not strongly formed and is difficult to see on most specimens. Genital pore anterior to bifurcation of gut, very close to oral sucker. Excretory pore posterior and dorsal, midway between ovary and posterior extremity of body. Eggs colourless, becoming opaque near distal end of uterus; small (0.018-0.020 mm internal length) and operculate with simple polar filaments up to 0.23 mm long (Fig. 11).

REDIA (Fig. 14)

Rediae at various stages of maturity present in haemocoeles of infected snails simultaneously. All are able to vary in size and shape considerably, though muscle contractions tend to be slow. Relaxed mature cercariae are up to 0.82 mm long by 0.27 mm wide. Two to five



Larval stages of *Notocotylus tadornae*.

Figure 14. Redia

Figure 15. Cercaria

Figure 16. Metacercaria

(all drawings based on photographs)

cercariae usually present within rediae, but normally two or three of these much larger than others. Larger cercariae are usually nearer anterior end of parent rediae, while several germ balls present in posterior end. Pharynx 0.052-0.058 mm wide, leading into a sac-like gut which extends back to about midway along body of rediae.

CERCARIA (Fig. 15)

Mature cercariae with opaque white bodies, ventrally concave, 0.23-0.29 mm long by 0.16-0.17 mm wide. Two lateral eyespots present and usually a median pigment spot. Tail translucent, 0.37-0.53 mm long, a postero-lateral appendage arising from the body on either side of tail. Measurements of live specimens are far more variable as mature cercariae are very active, constantly extending and contracting the body and beating the tail (Figs 17, 18 & 19). Immature cercariae (Figs. 20, 21) translucent except for a diffuse band of dark pigment across anterior third of body this being slightly more concentrated close to eyespots; tail shorter than in mature specimens though the body is usually longer. Excretory system of the Imbricata type described by Rothschild (1935) (see Fig. 22).

METACERCARIA (Fig. 16)

After emerging from *P. antipodarum,* cercariae swim until they find a surface suitable for encystment. Metacercariae are occasionally found on shells of live *Physastra variabilis* and *Potamopyrgus antipodarum,* but in natural conditions most are found on the undersurface of leaves of aquatic plants (Fig. 23). Encystment of cercaria was often observed under a microscope. The larva attaches to a suitable surface with the oral sucker and the body contracts to an almost circular shape. A clear cyst rapidly forms over the larvae, followed by a second inner layer. The tail lashes rapidly throughout encystment, and eventually breaks loose. (Fig. 24). The cyst slowly darkens until brown. Internal diameter of metacercarial cysts 0.137-0.155 mm (average 0.148 mm).

Figures 17-19. Mature cercariae of *Notocotylus tadornae* showing their ability to vary shape while alive.

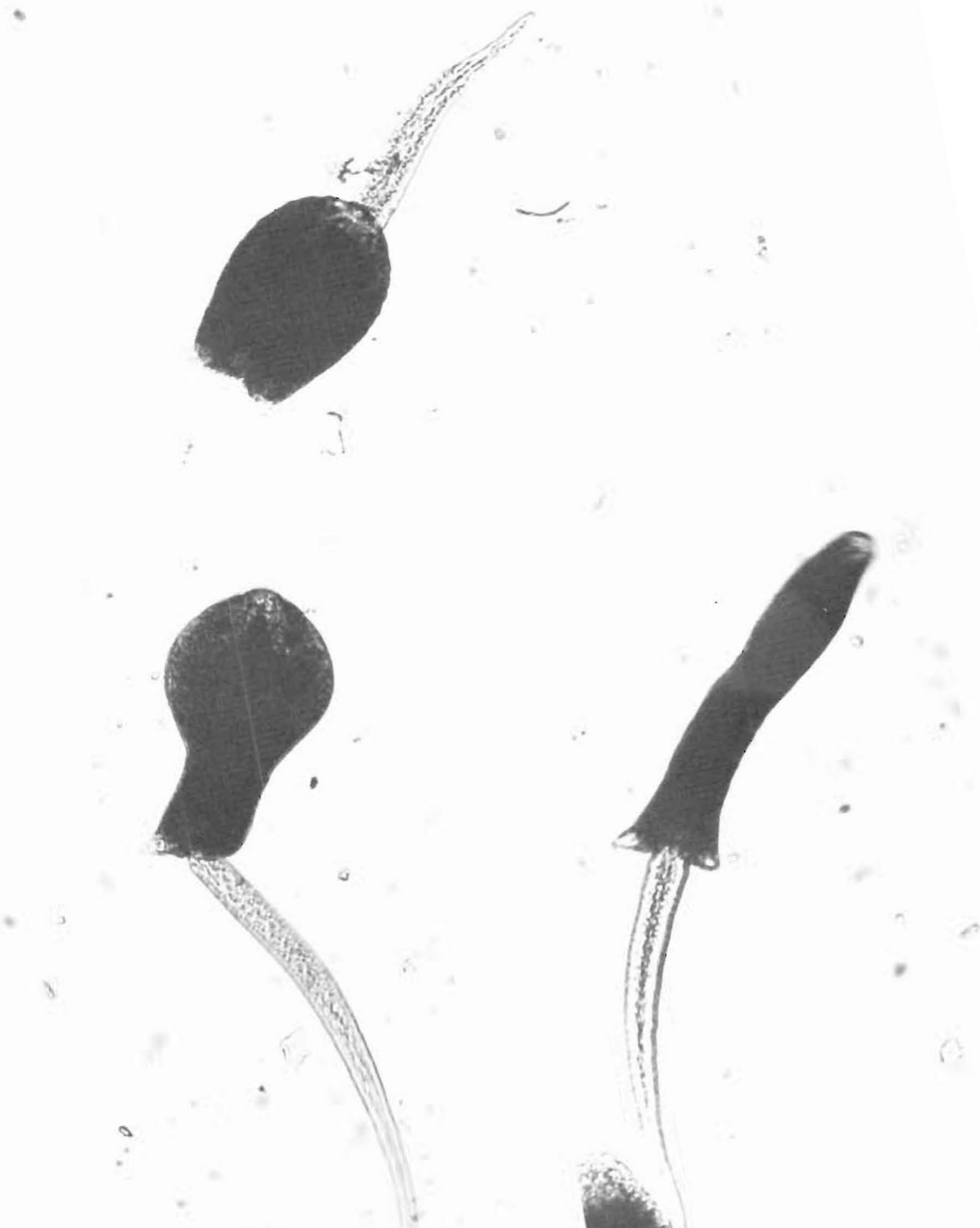
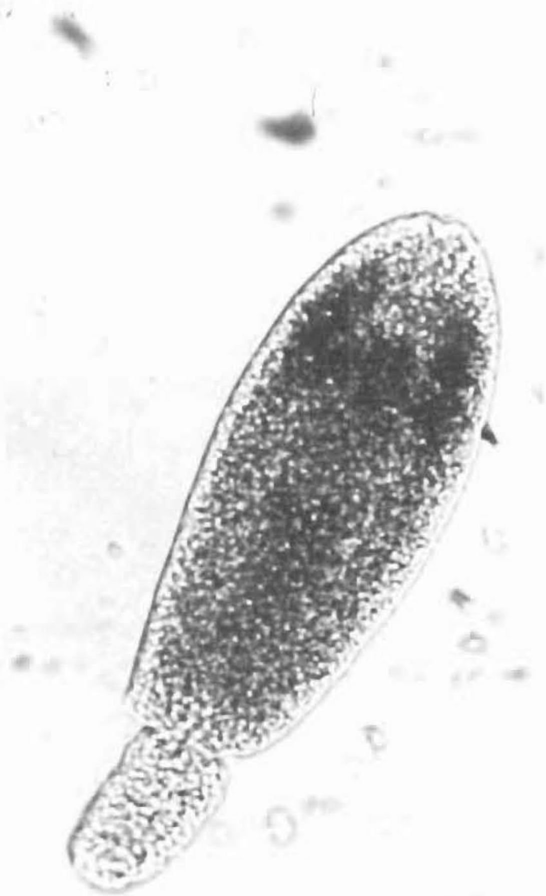


Figure 20. Very young cercaria probably not long out of mother redia. Note relatively long body and short tail.

Figure 21. Cercaria at a later stage of development. Note tail grown somewhat and anterior pigmentation more dense. Arms of the excretory system are visible in this specimen.

Figure 22. Anterior end of a nearly mature cercaria showing eyespots, and between them the Imbricata-type excretory system.



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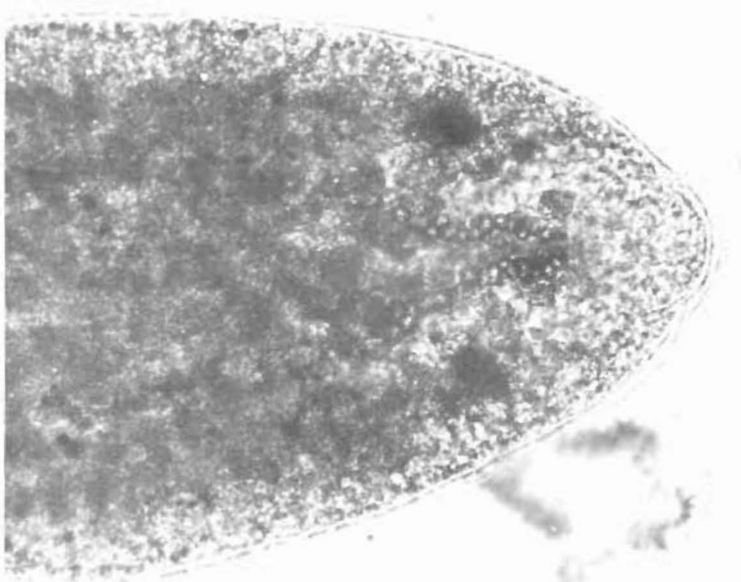

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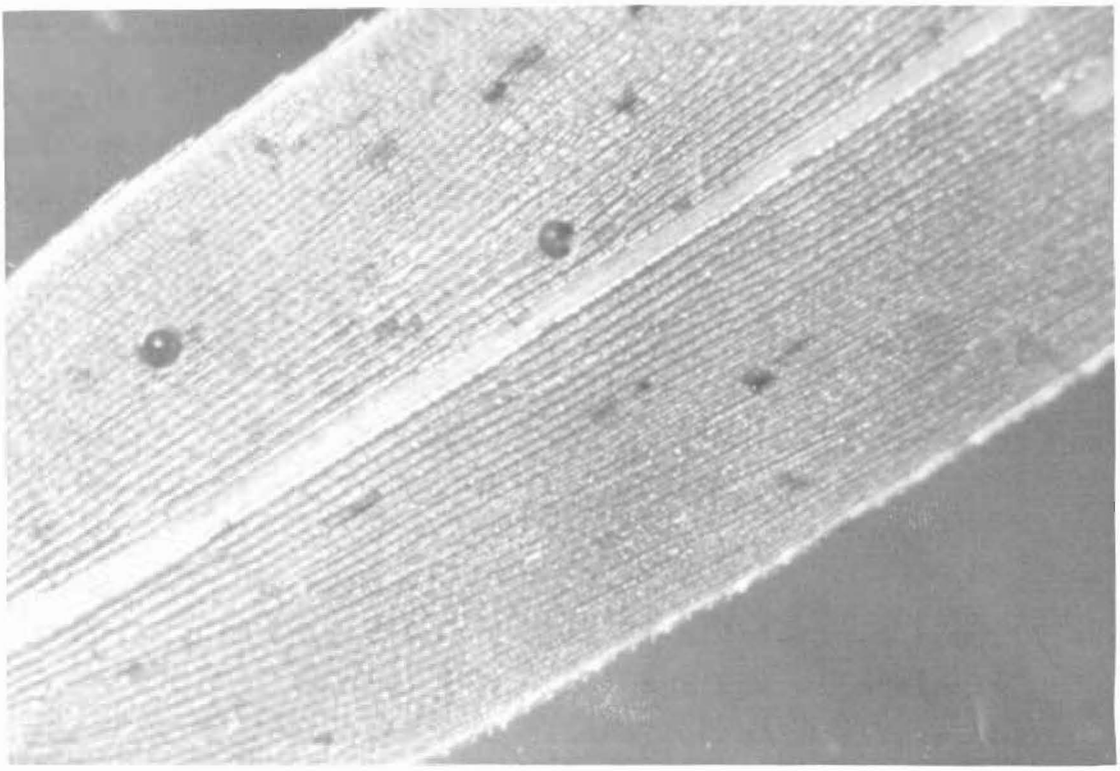
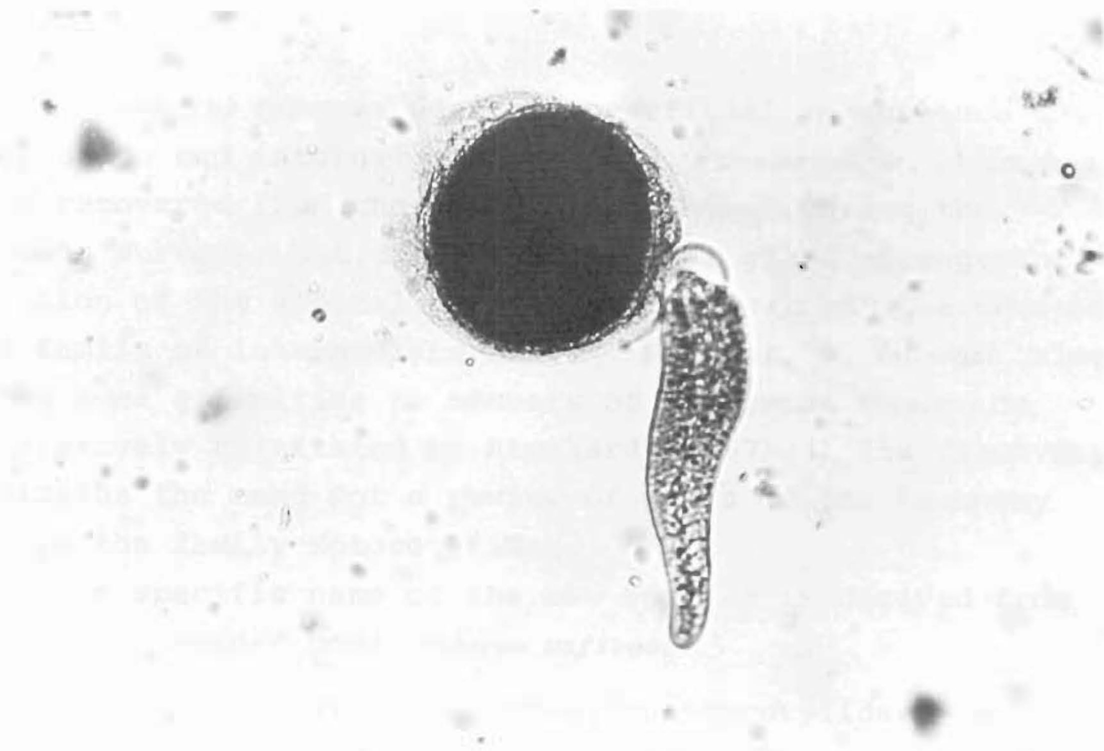
Figure 23. Notocotylid metacercariae are typically found on the undersurface of leaves of aquatic vegetation. Photo shows two metacercariae of *N. tadornae* on a leaf of *Elodea*.

Figure 24. An encysting metacercaria. The cyst wall has formed, but the tail still remains attached until it has lashed free.





MATERIAL EXAMINED

Holotype: 1 adult specimen
Paratypes: 29 adult specimens
Type Host: New Zealand Paradise Shelduck (*Tadorna variegata*, Gmelin)
Location: caeca
Type Locality: Hope River, Canterbury, New Zealand (N.Z.M.S. 1, Sheet S53); altitude 460 m.
Depository: To be deposited in the National Museum of New Zealand upon publication.

DIFFERENTIAL DIAGNOSIS

Notocotylus with more or less parallel-sided body, 1.46-1.92 mm x 0.47-0.65 mm. Ventral surface with single median row of seven sessile glands (occasionally eight). Cuticle spinous on ventral surface. Ratio of body length anterior to vitellaria to total body length 0.42-0.58. Genital pore anterior to bifurcation of gut caeca, close to oral sucker. Life cycle requires hydrobiid snail. Cercariae have Imbricata excretory system.

REMARKS

Notocotylus tadornae bears a superficial resemblance in body shape and internal anatomy to *N. attenuatus* (*N. attenuatus* also recovered from the caeca of *T. variegata* during the present survey), but differs in ventral gland arrangement, position of the genital pore (post-bifurcal in *N. attenuatus*) and family of intermediate host. However, *N. tadornae* also shows some affinities to members of the genus *Uniserialis* (tentatively reinstated by Stunkard, 1967). Its discovery indicates the need for a review of parts of the taxonomy within the family Notocotylidae.

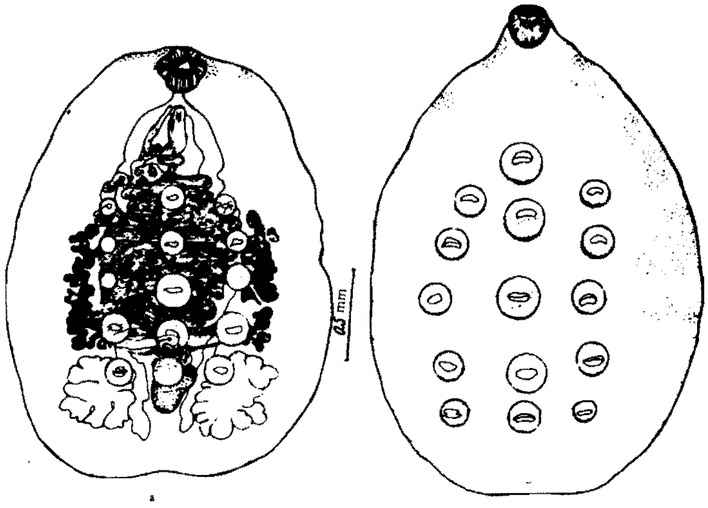
The specific name of the new species is derived from its only recorded host *Tadorna variegata*.

3) Taxonomy within the Family Notocotylidae

Several authors including Baylis (1928), Duthoit (1931), and Harwood (1939) have questioned the validity of basing genera of Notocotylidae on the differences of the ventral glands and ridges, but as yet no useful alternative characters have been suggested. Baer and Joyeaux (1961) provided the first step towards rectifying the situation by suppressing both *Uniserialis* and *Quinqueserialis* as being synonymous with *Notocotylus*. Stunkard (1967) tentatively reinstated the genus *Uniserialis* basing its separation from *Notocotylus* on cercarial characters and habitat of the adult. He added to the genus *U. breviserialis*, a new species with three rows of ventral glands.

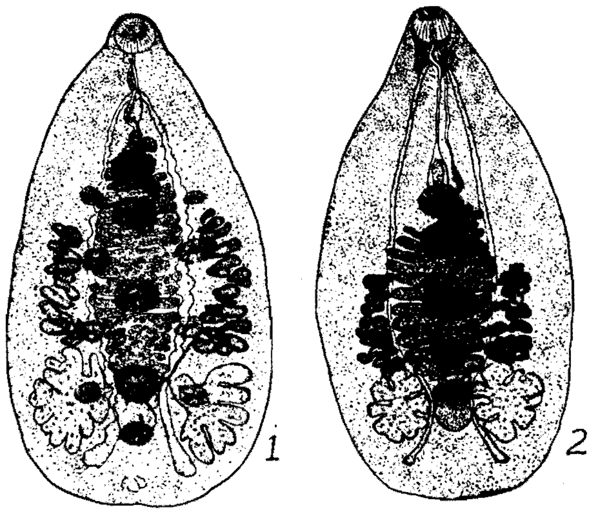
The discovery of *N. tadornae* during the present study provides further evidence against the basing of genera on the ventral gland arrangement. *Notocotylus tadornae*, having a single median row of seven ventral glands, would have fallen into the genus *Uniserialis* according to Beverley-Burton's (1961) key to the Notocotylidae. However, in overall body shape and habitat it appears much more closely related to species in the genus *Notocotylus* than to those in *Uniserialis*. It has the small body rounded at both ends typical of the genus *Notocotylus*, and like them occupies the caeca almost exclusively. *Notocotylus tadornae* was never found in the bursa during the present study. On the other hand, those species at present in the genus *Uniserialis*, are large and pyriform in shape, and occupy the bursa almost exclusively. Of the hundreds of *U. gippyensis* recovered during this study none were found in the caeca, although Beverley-Burton (1958) mentioned the presence of some specimens in the region.

There seem to be good grounds for retaining the genus *Uniserialis*, although the name may be inappropriate. Beverley-Burton (1958) remarked that *U. gippyensis* bears a superficial resemblance to *Notocotylus skrjabini* Ablasov, 1953, and this similarity is even more obvious between *N. skrjabini* and *U. breviserialis*. In addition, McDonald (1969) gave *N. skrjabini* as the only species of *Notocotylus* which inhabits the bursa of waterfowl. Because *U. gippyensis*, *U. breviserialis* and *N. skrjabini* form a unique group amongst the notocotylids (similar morphology and habitat which are both different from those of other notocotylids), it seems likely that they warrant a separate genus. A comparison of these three species with *Notocotylus attenuatus* and *N. imbricata* (Fig. 25) indicates why such a grouping is suggested and these can be compared with *N. tadornae* in Fig. 10.



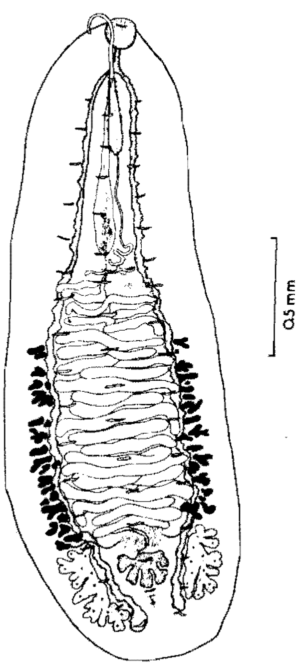
Notocotylus skrjabini

(reproduced from Ablasov, 1966)

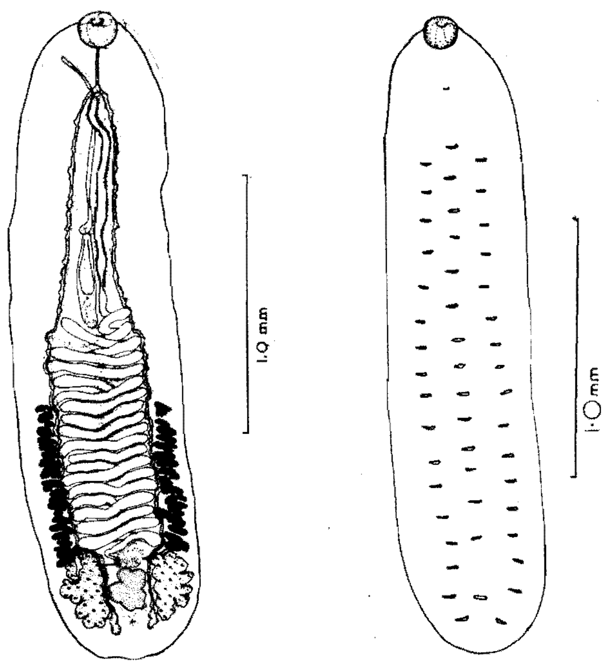


1. *Uniserialis breviserialis*
2. *Uniserialis gippyensis*

(reproduced from Stunkard 1967)



Notocotylus imbricatus



Notocotylus attenuatus

(reproduced from Beverley-Burton, 1961)

Figure 25. A comparison of notocotylids of the "Uniserialis group" with typical *Notocotylus* species.

The inclusion of *N. tadornae* in the Uniserialis group does not appear to be warranted despite some similarities between this species and *U. gippyensis*. The possession of a single median row of ventral glands by *N. tadornae* is shared only with *U. gippyensis* amongst the notocotylids, but the generic importance of this character has already been shown to be questionable. The similarity of the position of the genital pore in the adult worms, and the type of excretory system of the cercariae may be more important in linking *U. gippyensis* and *N. tadornae*, though no relationship has been established between types of cercarial excretory system and genera of the Notocotylidae. Until more is understood of the stability of various characters during the evolution of notocotylids, it is believed that the species described should lie within the genus *Notocotylus*.

IV. LIFE HISTORY OF *UNISERIALIS GIPPYENSIS*

Beverley-Burton (1958) described *U. gippyensis* from Mallards in England and created a new genus for the species. Her description was based on 49 specimens from three ducks. The biology of the life history was not investigated by her.

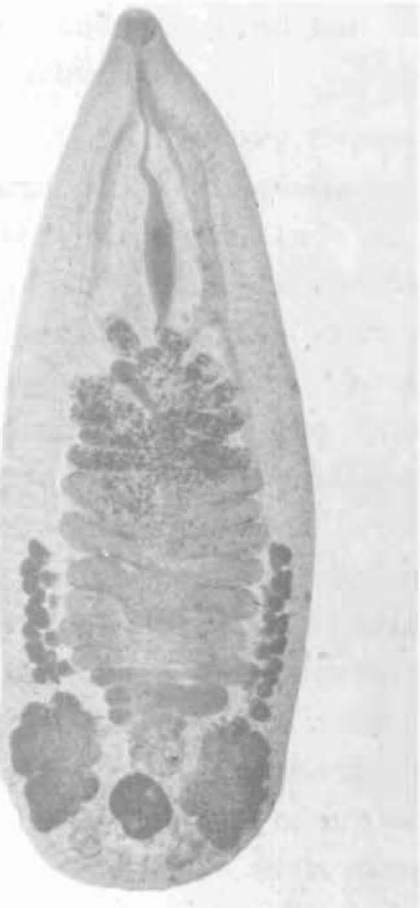
Uniserialis gippyensis is a very common parasite of the bursa of Fabricius of juvenile Paradise Shelducks - an infection rate of 76.5% was recorded amongst the juvenile birds taken throughout the study. The specimens examined fitted Beverley-Burton's description closely (see Figs. 26 and 27), although generally they tended to be larger than her description indicated (length of mature specimens varied between 2.26-3.70 mm). Although Beverley-Burton described her specimens as being aspinous, cuticular spines were present on the ventral surface of specimens examined in this study (Fig. 28). These spines appeared to be lost easily during fixation. No *U. gippyensis* were ever found in the caeca, although Beverley-Burton reported them from this location as well as the bursa.

Stunkard (1967) described a new species of notocotylid obtained from experimentally infected ducklings in America and proposed the name *Uniserialis breviserialis* for it. He also described the life history of the species, the intermediate host being a brackish water prosobranch snail

Figure 26. Internal structure of *Uniserialis gippyensis*.

Figure 27. Scanning electron micrograph of *U. gippyensis* showing the single median row of five large ventral glands.

Figure 28. Ventral surface of *U. gippyensis* immediately posterior to the oral sucker showing spinous cuticle, cirrus protruding from the genital pore and a recently extruded egg.



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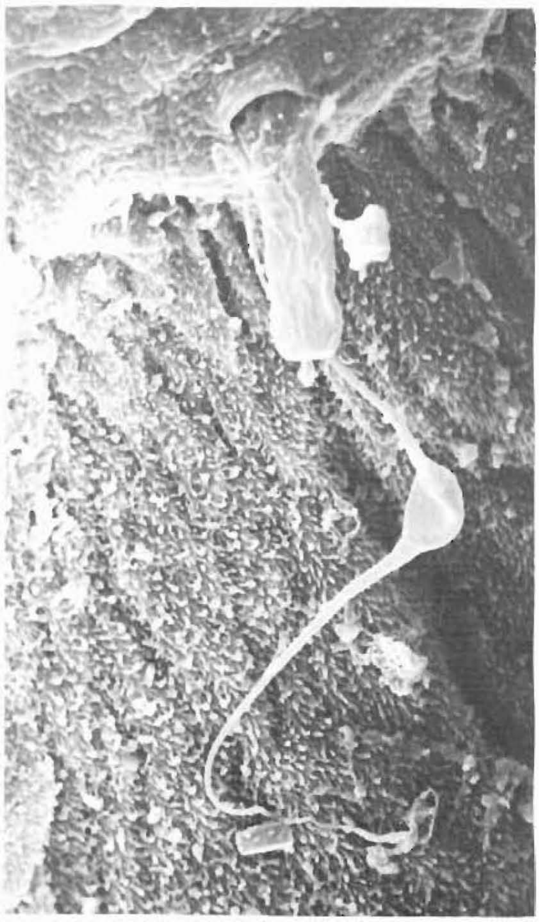

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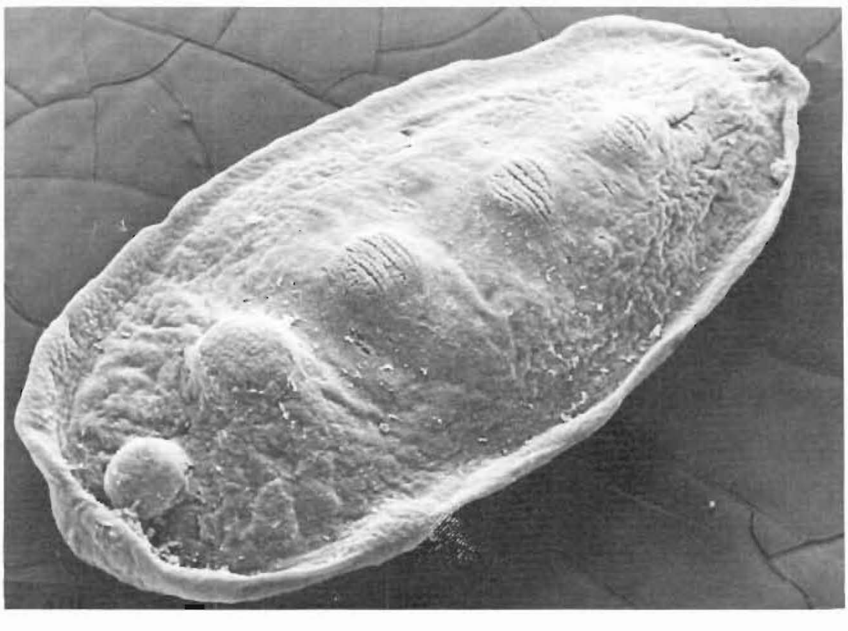

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Hydrobia salsa, and MacDonald (1969) suggested that the intermediate host species would be similar for *U. gippyensis.* A series of experiments was conducted as part of the present study to find the intermediate host of *U. gippyensis* in Canterbury.

1) Life History Experiments

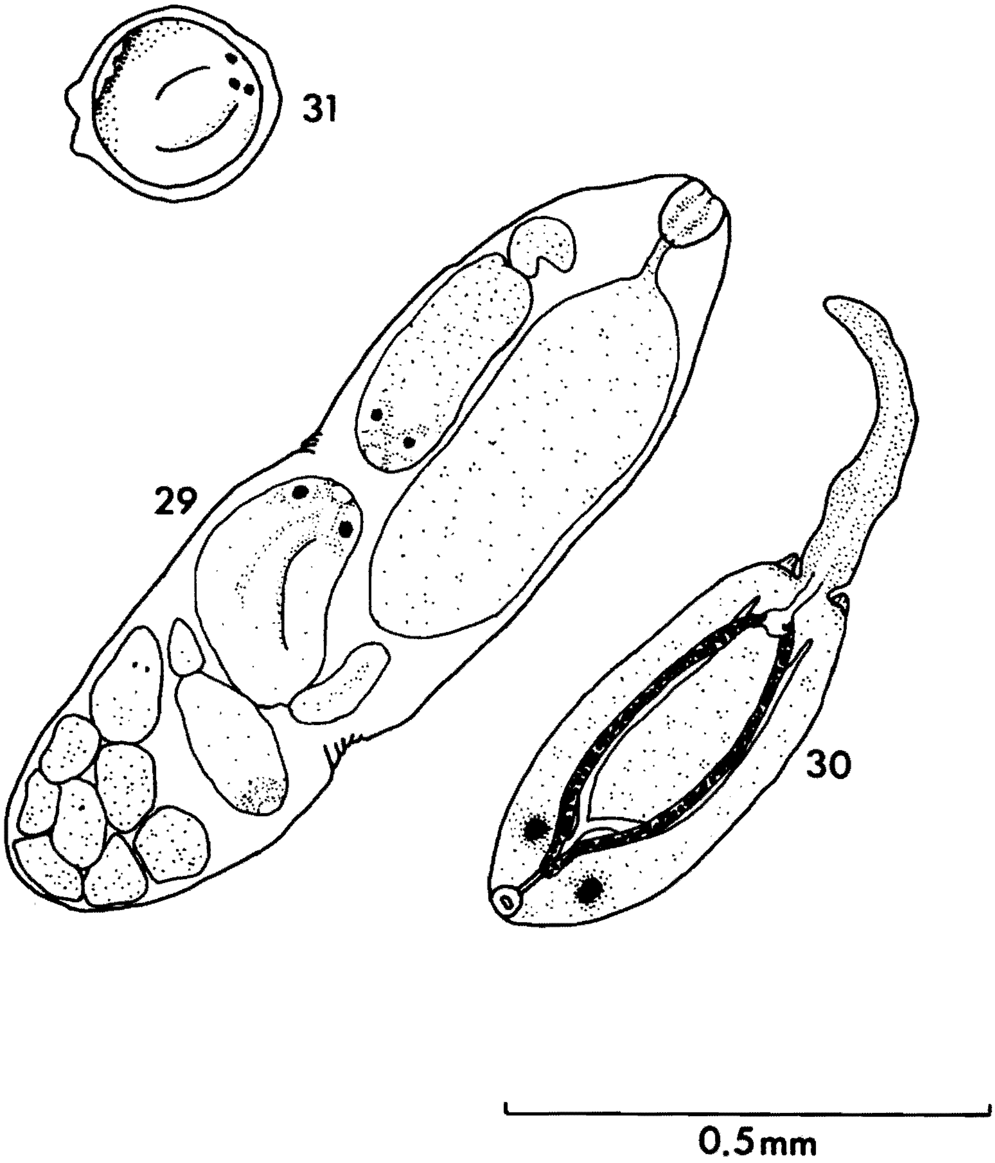
Eggs of *U. gippyensis* were placed into cultures of laboratory-bred snails - *P. antipodarum, G. corinna, P. variabilis, Physa* sp. and *S. novaezelandiae.* The eggs were normally teased from mature parasites with dissecting needles, but occasionally they were observed being extruded in ropy masses from the genital pore. The intermediate host of *U. gippyensis* was found to be *P. antipodarum,* a hydrobiid snail, and one of the commonest molluscs in the study area. No other snail species was successfully infected with *U. gippyensis.*

Metacercariae of *U. gippyensis* first appeared on the container walls and vegetation of the cultures of *P. antipodarum* 20-22 weeks after infection. These were collected and force-fed to incubator hatched ducklings on three occasions. In all cases adult *U. gippyensis* were recovered from the ducklings when they were killed and examined. Despite this, generally only a small proportion of the metacercariae fed to the ducklings developed - 28 adults were recovered from a duckling fed approximately 100 metacercariae, and one and 24 respectively from ducklings fed 50 each. All were recovered from the bursa of Fabricius of the ducklings, and 21 days were required for the parasites to mature.

2) Description of Larval Stages

REDIA (Fig. 29)

Body elongate, cylindrical, but shape and size can vary considerably with body contraction while alive. Relaxed mature rediae, distended with cercariae, up to 0.99 mm by 0.28 mm. Each contains from two to four cercariae usually in different stages of development. Several germ balls present at posterior end. Pharynx 0.058-0.063 mm wide, leads into a large sac-like gut which extends back almost half the length of the body.



Larval stages of *Uniserialis gippyensis*

Figure 29. Redia

Figure 30. Cercaria

Figure 31. Metacercaria

(all drawings based on photographs)

CERCARIA (Fig. 30)

Mature cercariae closely resembling those of *N. tadornae* though usually slightly larger. Body ventrally concave, 0.26-0.40 mm by 0.16-0.19 mm. Tail simple and translucent 0.51-0.60 mm long. Like those of *N. tadornae,* mature cercariae are very active though they swim for only a short time before encysting. Two lateral eyespots present (although a dark median spot of pigment often develops in addition to these in mature cercariae). Two postero-lateral appendages present. Body of young cercariae translucent, usually longer than mature specimens, though tail much shorter. Excretory system most easily seen in immature cercariae and is of the Imbricata type.

METACERCARIA (Fig. 31)

Metacercariae of *U. gippyensis* are formed in a similar manner to those of *N. tadornae* and similarly, under natural conditions, are usually found on the undersurface of leaves of aquatic plants near the surface of the water. The internal diameter of the cysts is generally between 0.145 and 0.164 mm with an average of 0.156 mm.

V. ECOLOGY OF NOTOCOTYLID LIFE HISTORIES

The life cycles of *U. gippyensis* and *N. tadornae* are very similar. Both species have similar larval forms, and both use the same intermediate host species - *P. antipodarum.*

This snail, by far the most numerous species in the study area and probably in most Canterbury shelduck habitats, appears to be widely used as an intermediate host by notocotylids in New Zealand. I have found by experimental infections, that *Catatropis* sp. can also use *P. antipodarum* as its intermediate host. Winterbourn (1974) described larval stages of four different forms of notocotylid from *P. antipodarum,* but I believe that two of these are questionable, and may be simply immature stages of one or both of the other two forms.

Infections of *N. tadornae* appear to be more common in *P. antipodarum* than are those of *U. gippyensis.* Six *U. gippyensis* and 19 *N. tadornae* were recovered from a young laboratory-reared duckling force-fed approximately 100 naturally encysted metacercaria collected from weed in a backwater of the Doubtful River. Metacercariae of *N. tadornae* were more numerous probably because a greater proportion of snails were infected with this species. This is to be expected when *U. gippyensis* is essentially restricted to juvenile birds.

Wright and Bennett (1964) stated that the eggs of *N. attenuatus* appear to have to be ingested by the snail host before they hatch. This is probably also true of *U. gippyensis* and *N. tadornae*. On two occasions a number of eggs of both species were kept for several weeks without showing signs of hatching. The factor which causes hatching is uncertain, but Wright and Bennett suggested that in *N. attenuatus* it is probably simply mechanical damage to the shell of the egg in the gut of the snail.

Like those of other notocotylids, the eggs of *U. gippyensis* and *N. tadornae* possess long polar filaments. Both the lack of a free-swimming miracidium and the possession of the polar filaments appear to have evolved in the group as an adaptation to infecting the snail hosts in moving water. The main advantage of the filaments seems to be their ability to anchor the egg in aquatic vegetation, thus increasing their chances of being ingested by a suitable snail host. Eggs of other species which do not possess filaments tend to sink and hatch when ready, the miracidia actively penetrating snails in the vicinity. Still or near still water would normally be necessary for this procedure to have greatest success.

Once infected by *N. tadornae* or *U. gippyensis* snails become reproductively sterile, but seem to survive well despite this. The period in the intermediate host is basically a multiplicative stage for the parasite and many cercariae are usually shed over considerable lengths of time. In the laboratory snails infected with *N. tadornae* and *U. gippyensis* in May were shedding cercariae by late October and were still doing so in June of the following year.

Encystment of metacercariae directly on aquatic vegetation is particularly well adapted for infecting grazing species such as the Paradise Shelduck. In terms of numbers and infection rates *N. tadornae* and *U. gippyensis* must be considered two of the shelduck's most successful helminths (see Chapter VI). There is little doubt that their success is a consequence of the closeness with which their life history ties in with the ecology of their host. While *N. tadornae* seems restricted in its choice of final host, *U. gippyensis* does not show such a high degree of specificity - Rind (1974) reported that it is present in at least five species of waterfowl in New Zealand.

VI. EVOLUTION OF *N. TADORNAE* AND *U. GIPPYENSIS*

Notocotylus tadornae is the commonest helminth parasite of the Paradise Shelduck, yet it has not been described previously. It therefore seems probable that it has evolved in New Zealand. *Uniserialis gippyensis* on the other hand was first described from Mallards in England (Beverley-Burton, 1958). Yet, since its description *U. gippyensis* has only been found in New Zealand. Because it is apparently so rare overseas and yet so widespread and common in New Zealand, it is probable that it also evolved here. If this is the case, it may have been carried to England in waterfowl species taken there for ornamental purposes. Alternatively it may have been carried there in *P. antipodarum*. Winterbourn (1970, 1972) showed that *P. antipodarum* and the European species *P. jenkinsi* are probably synonymous. He believed that the European snails were introduced from New Zealand (or possibly Australia) in the 19th century. It is possible that *U. gippyensis* is now spreading in Europe in the wake of the snail.

VII. LIFE HISTORY OF *CLOACOTAENIA MEGALOPS*

Cloacotaenia megalops is a cosmopolitan cestode, parasitic in waterfowl. It has been encountered in many studies of waterfowl parasites, but its life history and larval stages have been described only from northern Poland (Jarecka, 1958, 1960, 1961). *Cypris puberta* was the only intermediate host reported for *C. megalops*, and this ostracod is unknown from New Zealand (Eagar, 1971).

Cloacotaenia megalops is very common in the Paradise Shelduck and so it seemed probable that its normal intermediate host species was also relatively common in the shelduck's habitat. *Herpetocypris pascheri* Brehm, 1929, a freshwater ostracod was particularly common throughout slow-flowing and still waters in the study area, and *Cyclops* spp. were present in still waters (Dr V. Stout kindly verified identification of the ostracod). Thus, these species were the most obvious to test in the life history experiments.

Eggs from the ripe proglottids of several *C. megalops* were added to cultures of laboratory-bred *H. pascheri* and unidentified *Cyclops* sp. The cultures were maintained for 21 days, when they were inspected for infection. Of 10 ostracods selected at random from the culture, eight were found to be infected with an average of 2.3 cysticercoids of *C. megalops* (Fig. 32). None of the *Cyclops* was infected. Although other *H. pascheri* were successfully infected subsequently, two attempts at infecting incubator-hatched Khaki-Campbell ducklings were both unsuccessful.

Nevertheless, from the high success rate of experimental infections, it is believed that *H. pascheri* is a natural transmitting agent of *C. megalops* in the study area and is probably used as such throughout the country - Chapman (1963) stated that *H. pascheri* is the most widely distributed ostracod in New Zealand. A number of other ostracod species are also found throughout the country - Chapman (1963) listed 26 living freshwater species and Barclay (1968) gave five additional species. It is possible that some of these are also involved in transmitting *C. megalops*.

It seems unlikely that copepods are involved in the life history of *C. megalops*. Jarecka (1961) working in the Lakes District of northern Poland, found that while *C. megalops* would invade *Cypris puberta*, an ostracod, negative results were obtained for experimental invasions of the copepods *Macrocyclops albidus*, *N. fuscus* and *Acanthocyclops viridis* and the ostracods *Cypridopsis vidua* (which is present in New Zealand,

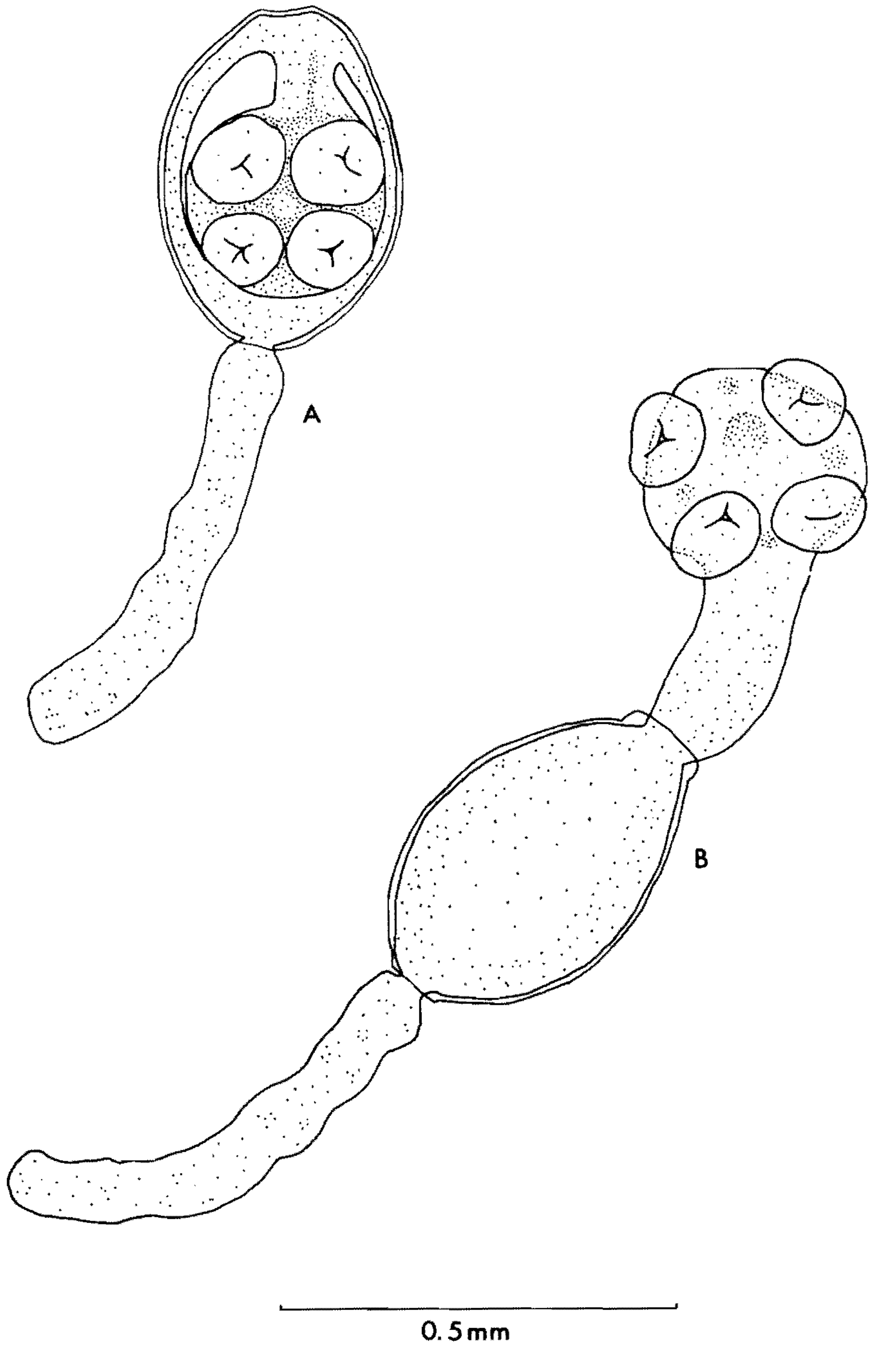


Figure 32. A. Cysticercoid of *Cloacotaenia megalops*
B. After evagination
(drawings based on photographs)

Barclay, 1968) and *Notodromas monashi*. He suggested that the specificity that he found in relation to the ostracod species was due to differentiation of biotopes of ostracods in natural conditions. Eggs of *S. megalops* are thick walled and heavy and sink to the bottom where they are readily picked up by benthic ostracods (Jarecka, 1961). This explanation fits in well with the ecology of *H. pascheri*, which is a poor swimmer and appears to feed mainly amongst the deposit of detritus on the bottom of still or slow-flowing pools.

Despite their benthic feeding habits, *H. pascheri* have a tendency to gather around plant material. This was observed in the laboratory breeding colonies, where the largest numbers were usually found amongst filamentous algae and aquatic moss. In natural conditions the percentage of these ostracods infected with *C. megalops* is probably low (despite examination of many *H. pascheri* no naturally infected specimens have been found) and thus, their tendency to gather amongst vegetation would facilitate a higher success rate for the infection of a phytophagous host species such as the Paradise Shelduck, than would otherwise have been expected.

VIII. A REVIEW OF THE LIFE HISTORIES OF THE OTHER HELMINTHS OF *T. VARIEGATA*.

Life histories of most of the species of helminths found in *T. variegata* during this study have been documented previously. The following section presents some of the information found in overseas studies and suggests likely hosts in New Zealand.

1) Cestodes

a) *Fimbriaria fasciolaris* - Jarecka (1961) reported that the intermediate host of *F. fasciolaris* is generally a copepod, although Garkavi (1950) found cysticercoids of this species in an amphipod *Gammarus* sp. A surprisingly large number of genera are reported to be capable of acting as intermediate hosts for *F. fasciolaris*. In Europe copepod genera found naturally infected with cysticercoids of *F. fasciolaris* are *Macrocyclops, Acanthocyclops, Eucyclops, Cyclops,* *Mesocyclops,* and *Diaptomus* (Jarecka, 1961; Joyeaux and Baer, 1936; and J. Neradová-Valkouriová, 1971). Several others have been infected experimentally. Thus, while the species is generally restricted to copepod intermediate hosts, it does not seem very host-specific within this group.

During the present study attempts were made to infect both *Herpetocypris pascheri* and *Cyclops* sp. with *F. fasciolaris,* but both were unsuccessful. However, it seems certain that, as in Europe, *F. fasciolaris* utilises copepods as intermediate hosts in New Zealand. A number of copepod species are present and any of these - particularly the cyclopoideans - are possible hosts.

With reference to cyclopoideans, Marples (1962) wrote, "While they do occur in mid-winter, they are most commonly found moving jerkily near the bottom or amongst vegetation." This could be an important factor in the transmission of *F. fasciolaris* to the shelduck. As *T. variegata* is basically a phytophagous species, it is doubtful that it would deliberately eat sufficient numbers of copepods to account for the number of parasites present unless they were taken in with aquatic plant food.

b) *Aploparaksis furcigera* - The intermediate host of *A. furcigera* in Europe is an oligochaete *Limnodrillus* sp. (Jarecka, 1960). In New Zealand, the intermediate host is probably also one or more of the numerous freshwater oligochaete species. Only two very young shelducks were parasitised by *A. furcigera,* yet the species is common in the Grey Duck and Mallard (see Chapter VII). Differences in feeding habits are almost certainly responsible for the differences seen in infection rates of these species. The Paradise Shelduck, being basically a grazer, would be unlikely to consume many aquatic oligochaetes as these are mainly mud-dwellers.

c) *Anomotaenia ciliata* - Jarecka (1958, 1961) found that cysticercoids of *A. ciliata* develop in the planktonic cladoceran crustacean *Simocephalus exspinosus* in Poland. This cladoceran genus is represented in New Zealand by four species (Marples, 1962). It is therefore likely that cladocerans - particularly *Simocephalus* spp. - act as intermediate hosts in the study area. Although a number of unidentified cladocerans were examined for larval cestodes, none was found infected. As is the case for the intermediate hosts of many cestode species, the chances of infected planktonic cladocerans being ingested by shelducks is probably low. This almost certainly explains the rarity of *A. ciliata* in the shelducks examined. However, the species is more common in "dabbling ducks" from the study area (see Chapter VII).

d) *Sobolevicanthus gracilis* - This is a cosmopolitan species whose life history is well known. McDonald (1969) lists 23 freshwater crustacean species known to be intermediate hosts of this cestode. Twelve of these are copepods, but in general *S. gracilis* is more frequent and develops faster in ostracods than in copepods (McDonald, 1969). Eight of the copepod species utilised by *S. gracilis* are also known to be intermediate hosts of *F. fasciolaris.*

2) Trematodes

a) *Cotylurus cornutus* - Many authors, working in various countries, have studied the life history of *C. cornutus.* McDonald (1969) listed them and gave a summary of their findings. Briefly the life history of *C. cornutus,* like those of most strigeids, includes two intermediate hosts. The first is generally a snail of either the genus *Lymnaea* or *Planorbis,* while the second may be one of a number of species of snail, leech or oligochaete. Eggs, in the faeces of the definitive host, are passed into water, where they hatch into miracidia, invade the first intermediate host and develop into rediae. Cercariae develop within the rediae and eventually emerge to penetrate a second intermediate host where they develop into metacercariae. Metacercariae develop into adults in the definitive host within two days of the ingestion of the second intermediate host. The whole life history can be completed in 2½-4 months.

Lymnaea stagnalis and *Planorbarius corneus* are both known to be used by *C. cornutus* as first and second intermediate hosts (McDonald, 1969), and both these species of snails have been introduced into New Zealand, but for the most part are present only in small localised populations - *Planorbarius* only in the North Island (Winterbourn, 1973). It is therefore doubtful that they are major transmitters of *C. cornutus* to the Paradise Shelduck. *Cotylurus cornutus* has been found to be capable of using *Gyraulus corinna* as its first and second intermediate hosts (S. Rind, pers. comm.), and this snail is much more widespread than *Lymnaea stagnalis.* Thus it is probable that *G. corinna* is a major source of infective larvae of *C. cornutus* for Paradise Shelducks in the study area. *Gyraulus corinna* is usually found on aquatic vegetation - an important factor for the successful transmission of the infective larvae to a grazing definitive host.

b) *Echinostoma revolutum* - McDonald (1969) listed 37 published studies on the life history of *E. revolutum.* The typical pattern of development of this species is therefore well known. The life history of *E. revolutum* is basically similar to that of *C. cornutus.* Eggs are passed in the faeces of the definitive host. They hatch into miracidia which penetrate freshwater snails (generally planorbids, physids or lymnaeids), where development of cercariae takes place in about 39 days. They then emerge and penetrate a second intermediate host or re-enter their first. A much greater variety of species are reported to act as second intermediate hosts. The second host may be a mollusc, planarian, tadpole, or fish. The cercariae encyst in this host, where they remain until ingestion by the definitive host initiates development of the adult parasite.

No work has yet been published on the life history of *E. revolutum* in New Zealand. *Lymnaea columella, L. stagnalis* and *Planorbarius corneus*, which are known to act as intermediate hosts of *E. revolutum,* have all now established wild populations in New Zealand. None however, are common species in the South Island. *L. columella* is restricted to the Nelson province, and to areas of swamp just south of Timaru, while *L. stagnalis* is more widespread but still comparatively rare in Canterbury and is apparently not present in the high-country (Pullan, Climo and Mansfield, 1972). *Planorbarius corneus* is present only in the North Island. These species are probably therefore not responsible for transmitting any of the *E. revolutum* infections found in the study area. However, it is known that *Gyraulus corinna*, a planorbid snail, can act as both first and second intermediate hosts, and that *Physa* sp. can be utilised as the second intermediate host (S. Rind, pers. comm.). While the potential non-mollusc intermediate hosts mentioned above may play a part in the transmission of *E. revolutum* to Paradise Shelducks, it is likely that *G. corinna* is the major transmitter in the study area. Despite examination of many *G. corinna* from the study area, no echinostome intermediate stages were found.

c) *Hypoderaeumconoideum* - The life history of *H. conoideum* is typically echinostome in form. The only major difference from that of *E. revolutum* is that apparently a much narrower range of intermediate hosts can be utilised. With the exception of *Planorbarius corneus*, only snails of the genus *Lymnaea* have been reported to act as first intermediate hosts of *H. conoideum* (McDonald, 1969). While a greater variety of species are utilised as second intermediate hosts, only mollusc species have been reported. Of the genera reported to be used *Gyraulus, Lymnaea, Physa, Planorbarius, Pisidium* and *Sphaerium* are represented in New Zealand. However the distribution of *H. conoideum* may be limited by the narrow choice of first intermediate host.

Only one shelduck was found to be infected with *H. conoideum* during the study. This was a juvenile bird, barely fledged, which was collected in a swamp where *Lymnaea tomentosa*, an endemic lymnaeid was very numerous. Although approximately 30 specimens of *L. tomentosa* were collected from the swamp and examined, none was found to be infected with any echinostome larvae. Nevertheless, it does seem likely that *L. tomentosa* was acting as an intermediate host to *H. conoideum* in the study area.

d) *Echinoparyphium recurvatum* - The life history of *E. recurvatum* is similar in form and development time to that of *E. revolutum* and *H. conoideum.* McDonald (1969) lists snails of several genera which have been recorded as first intermediate hosts of the species. Those represented in New Zealand are *Gyraulus, Lymnaea* and *Physa*. Additional molluscan genera can act as second intermediate hosts, and of these *Planorbarius, Pisidium* and *Sphaerium* are represented in New Zealand. Metacercaria can also develop in the kidneys of the frog tadpoles, though it is doubtful if these are a normal source of *E. recurvatum* infections for Paradise Shelducks. *Lymnaea stagnalis* is the only species present in New Zealand which is reported to act both as first and second intermediate hosts of *E. recurvatum* (McDonald, 1969). However, because of the extremely limited distribution of *L. stagnalis*, it is probable that as for *C. cornutus* and *E. revolutum, G. corinna* is the major source of infection for shelducks.

e) *Echinostoma* sp. - It is likely that this species has a life history very similar to that of *E. revolutum,* and probably uses the same intermediate hosts.

f) *Notocotylus attenuatus* - Extensive studies on the life history of *N. attenuatus* have been carried out in several countries (McDonald, 1969), and consequently it is well known.

Eggs of *N. attenuatus* are ingested by freshwater snails as is the case for *N. tadornae* and *U. gippyensis*. Cercariae have been reported to develop in about seven weeks. Metacercariae encyst on a variety of substrates likely to be ingested by final hosts. Williams (1966) reported that if eaten, infected snails can also be infective. Species which have been found to act as intermediate hosts to *N. attenuatus* are mainly lymnaeids.

Notocotylus attenuatus is relatively uncommon in both Paradise Shelducks and other waterfowl species in the study area. If it utilises lymnaeid snails in New Zealand as it appears to elsewhere, then this could be the reason for its rarity. There is further evidence which suggests strongly that this is the case. Of the six shelducks found with infections of *N. attenuatus* during the study, five were collected from an area of swamps in the headwaters of the Boyle River. These swamps were the only place in the study area known to support large populations of *Lymnaea* *tomentosa*. Few if any *P. antipodarum* existed in this swamp. Thus, it seems likely that *L. tomentosa* was responsible for transmitting *N. attenuatus* to the shelducks.

g) *Dendritobilharzia pulverulenta* - The life cycle of *D. pulverulenta* is unknown. However, MacFarlane (1949) studying "bather's itch" in the Southern Lakes of New Zealand, found that the irritation was due to the penetration of schistosome cercaria. The New Zealand Scaup (*Aythya novaeseelandiae*) and the Grey Duck (*Anas superciliosa*) were common waterfowl in the infected areas, and it is probable that both acted as hosts to the schistosome. MacFarlane successfully infected a New Zealand Scaup with the schistosome, and whilst schistosome eggs were passed by the duck, the adult parasite was not retrieved and identified by him. He examined several species of snail from infected areas - *Physastra variabilis, Potamopyrgus antipodarum, Sphaerium novaezeelandiae, Lymnaea tomentosa* and *Lymnaea alfredi*. Only the two lymnaeids were found to be infected with furcocercous cercariae.

Grey Ducks, Mallards and Paradise Shelducks in Canterbury are infected with *D. pulverulenta,* and this is possibly the same species studied by MacFarlane (1949). While the species is not abundant in Paradise Shelducks it is certainly in a higher proportion of the birds than results of this study indicate, as it was never intensively searched for. This suggests that a snail species other than the lymnaeids may also be involved in transmission. *Gyraulus corinna* could fill this role.

h) *Typhlocoelum* sp. - Because no mature specimens of *Typhlocoelum* sp. were obtained from the Paradise Shelducks, no specific identification could be made. The life history is known for only one species of *Typhlocoelum* found in waterfowl. This is a cosmopolitan species, *T. sisowi*. It needs only one intermediate host which is usually a lymnaeid or planorbid snail (McDonald, 1969).

3) Nematodes

a) *Capillaria anatis* - The life history of *C. anatis* is direct with a prepatent period of 28 days (Wetzel and Quittek, 1940). The eggs are passed onto the ground with the host's faeces and are picked up by another grazing host at a later stage. Paradise Shelducks, particularly non-breeding birds, tend to congregate on areas of good grazing in the study area. Quite often these areas become badly fouled. This provides good conditions for the transmission of *C. anatis*. Even within the territories of adult pairs there are undoubtedly good feeding areas to which the birds return many times, and thus sources of infection are probably equally available to both breeding and non-breeding birds.

b) *Porrocaecum crassum* - Whilst this species is common in waterfowl throughout Eurasia (McDonald, 1969), information on its life cycle has been published only in Russia.

The eggs embryonate after they have passed out with the host's faeces. They hatch and larvae develop after ingestion by a terrestrial earthworm or dipterous insect larva. The adults mature three weeks after ingestion by the definitive host.

The diet study of the Paradise Shelduck (Chapter III) indicates that a number of species of dipterous larvae are ingested with aquatic vegetation. These are a possible source of infective larvae of *P. crassum*. While earthworms were not recovered from the shelducks, it is recognised that these break down very quickly. Paradise Shelducks probably eat some earthworms, particularly after rain when many earthworms come to the surface. Both dipterans and oligochaetes are plausible sources of infection.

c) *Epomidiostomum uncinatum* and *Amidostomum acutum* - The life histories of these two closely related species are very similar. Neither require intermediate hosts. Eggs are passed out with the faeces of the host. Larvae hatch in water and are infective to the final host in 5-11 days (Leiby and Olsen, 1965). Paradise Shelducks would ingest infective larvae of these species during their normal activities of drinking and eating from shallow ponds and backwaters.

d) *Trichostrongylus tenuis* - *Trichostrongylus tenuis* has a direct life cycle (McDonald, 1969). Eggs are passed with the faeces and hatch in the soil. Larvae become infective after six to seven days, when they migrate up plants. They mature four to seven days after ingestion by the definitive host.

e) *Tetrameres* sp. - McDonald (1969) lists the intermediate hosts so far recorded for *T. fissispina*. They include species of marine and freshwater amphipod, isopod, cladoceran and ostracod crustaceans, insects, flatworms and oligochaetes. Further work may reveal other host species. It is probable that other species of the genus *Tetrameres* can also be transmitted by a wide range of intermediate hosts. Most of the groups listed as intermediate hosts of *T. fissispina* are represented in the shelduck's habitat.

IX. CONCLUSIONS

The helminths of the Paradise Shelduck can be divided into four categories on the basis of how they achieve infection of their final host:

1) Those species whose infective stages encyst on aquatic vegetation.
2) Those whose infective stages encyst in secondary intermediate hosts.
3) Those whose infective stages actively penetrate their definitive host's tissue.
4) Those species with direct life histories.

The life cycles of *U. gippyensis, N. tadornae* and *N. attenuatus* (those species which fall into the first category), appear to be better suited to infection of Paradise Shelducks than those of any of the other helminths present. In the case of *N. attenuatus* however, the availability of a suitable intermediate host could be a limitation. On the other hand, *P. antipodarum,* the host snail of *U. gippyensis* and *N. tadornae,* is the most abundant and most widespread snail in the study area. However, their means of reaching the final host is just as important to their success. By possessing metacercariae which encyst on aquatic vegetation they are successful in achieving transmission to an almost wholly vegetarian host.

Most of the shelduck's other helminths whose life cycles are indirect, require the ingestion of their intermediate host for transmission. Normally adult Paradise Shelducks do not actively seek aquatic invertebrates as a part of their diet. Most of those which are ingested are taken in accidentally along with aquatic vegetation. Only a very small proportion of the birds were found to dabble (see Chapter III). It is probable that the species in the second group have not evolved with a grazing host, but utilise such a host when the opportunity arises. The effectiveness of life histories of trematodes in this group is increased by extremely prolific secondary multiplicative phases within the intermediate hosts. Although lacking such phases in the intermediate hosts, the cestodes cope by possessing a particularly prolific system of sexual reproduction, and often a longer life in the definitive host. Nematodes with an indirect life history are rare in Paradise Shelducks.

In the study area only larvae of *Dendritobilharzia pulverulenta* appear to actively penetrate the shelduck. Paradise Shelducks spend much of their time grazing on terrestrial vegetation. The time spent by the shelducks on water may well be a limiting factor as far as *D. pulverulenta* is concerned.

The nematodes which have a direct life history, are most successful when host densities are high, as they lack a secondary multiplicative phase. The species in this group are well suited to hosts which form large feeding flocks as does the Paradise Shelduck. Flocks of up to 300 birds were seen on collecting trips, but due to an increase in area of exotic pasture and a simultaneous but unrelated decline in the shelduck population, concentrations of shelducks have been reduced to some extent over the last decade.

CHAPTER VI

QUANTITATIVE ASPECTS OF HELMINTH INFECTIONS IN *T. VARIEGATA*

I. INTRODUCTION

Many papers have been published on the morphology and systematics of wildfowl parasites. but until recently few have dealt in detail with the quantitative aspects of the infections. Papers by Gower (1938), Bezubik (1956), Cornwall and Cowan (1963), Buscher (1965), Avery (1966a & b), Kinsella and Forrester (1972) and Beverley-Burton (1972) are the main studies covering this field. These studies concern wildfowl of the Northern Hemisphere (Europe and North America), and except for those of Avery (1966b) and Kinsella and Forrester (1972), all deal with species which are migratory. None concerns shelducks or other grazing species.

The aims of this section of the study were:

1) To see how heavily Paradise Shelducks in their natural habitat are infected with helminths.
2) To see if the younger birds are more heavily parasitised than the adults, as in many other vertebrate species.
3) To see if there are any sexlinked differences in infections.
4) To find how the worm burdens vary throughout the year.

The terms incidence and intensity used throughout this chapter refer to the percentage of birds infected in the sample, and the mean number of helminths per infected birds, respectively.

Data from all shelducks taken during the study period are not used in section II of this chapter, because it is believed that they cannot be meaningfully combined irrespective of time of year. Changes in the incidence and intensity of invasions occur during the year, but it is uncertain if exactly the same patterns recur annually. For this reason section II is based on data obtained from birds collected in May only (the shooting seasons of 1971-

1973). These birds, however, represent a substantial proportion of the total sample (181 in all were collected during these shooting seasons). Section IV is based on the samples of 10 birds per month taken under permit throughout the study.

II. INFECTIONS OF THE LOWER GASTRO-INTESTINAL TRACT DURING MAY

Ducks collected during May contained most of the helminth species found. Those species that were found only outside May, were generally found in very young ducks, which appear to be susceptible to unusually large and diverse helminth infections (see section III).

Very few of the shelducks examined were entirely free of helminths. Of the 181 birds collected in the May samples the lower tracts of only four were free of helminths representing an overall infection rate of 97.8%, while the mean number of helminths per infected bird was 46.4. However, the variety of helminths simultaneously inhabiting the viscera of each shelduck was not great - an average of only 3.17 species per bird were present. Trematodes as a group were the most frequently encountered helminths, followed by cestodes and nematodes respectively (see Table 5). The high incidence of trematodes is mainly a consequence of the high frequency of infection by the notocotylid trematodes *U. gippyensis* and *N. tadornae*. *Notocotylus tadornae* was not only the most commonly encountered parasite species (68.0% of all shelducks collected in May), but the intensity of infection by this species also tended to be high. During May the largest single burden of *N. tadornae* consisted of 444 individuals, but the largest burden over the whole study consisted of 2160 individuals in a duck collected in February 1973. Of the birds in the May samples, 49.2% were infected with the other common species of notocotylid - *U. gippyensis*. However, because this species is, with few exceptions, restricted to juvenile birds, the incidence rate expressed as a percentage of the entire May sample can only reflect the proportion of adults and juveniles in the sample and not the true percentage incidence in hosts available for infection. For this reason it is probably more meaningful for the incidence of *U. gippyensis* to be expressed as a percentage of the juveniles present only. Nearly 80% of juveniles were infected. The largest infection by *U. gippyensis* recorded from the May samples consisted of 34 individuals, but this number was exceptional as the average number per infected bird was 5.15 (S.D. of 5.29). Throughout the rest of the study only one burden of *U. gippyensis* was of greater size - one young shelduck collected during December 1972 contained 131 of this species. The only other notocotylid found inhabiting the Paradise Shelduck was *N. attenuatus*. One bird, which carried 160 individuals was the only shelduck from the May samples which was infected by this species.

Cotylurus cornutus was found parasitising the shelducks reasonably frequently, but sizes of infections were always small. In May, numbers ranged up to only seven. This was the largest infection by this species found throughout the entire study.

Two of the three species of echinostome present were regular parasites of Paradise Shelducks. *Echinoparyphium recurvatum* was found quite frequently, though not usually in very large numbers, while *Echinostoma revolutum* was less frequently found and burdens were even smaller than those of *E. recurvatum* (see Table 6). Three specimens of a third unidentified echinostome were found infecting a young female in May. The species was found on only one other occasion - a single specimen was found in a young female in January.

Only two species of cestode were commonly present in the shelducks inspected - *Cloacotaenia megalops* and *Fimbriaria fasciolaris* - and these were the only cestodes present in the May samples. *Cloacotaenia megalops* was present in a large number of the birds. Over 60% of the shelducks were infected with this species, although infected birds averaged only 4.0 specimens each. The largest infection by *C. megalops* was 16, found in a bird collected in May 1971. The relatively low intensity of most infections by

Table 6. HELMINTH INFECTIONS OF THE LOWER GASTRO-INTESTINAL TRACTS OF 181 PARADISE SHELDUCKS DURING MAY

	number infected	% incidence	total no. parasites	intensity (no./infected bird) mean	range	diversity (no. spp. /bird) mean	range
TOTAL CESTODES	138	76.2	792	5.74	1-54	1.03	0-2
C. megalops	111	61.3	440	3.96	1-16		
F. fasciolaris	76	42.0	352	4.63	1-52		
TOTAL TREMATODES	158	87.3	6974	44.14	1-447	1.64	0-5
U. gippyensis	89	49.2	458	5.15	1-34		
N. tadornae	123	68.0	5921	48.14	1-444		
N. attenuatus	1	0.5	160	160	160		
E. revolutum	18	9.9	33	1.83	1-7		
Echinostoma sp.	1	0.5	3	3	3		
E. recurvatum	25	13.8	320	12.80	1-178		
C. cornutus	39	21.5	79	2.03	1-7		
TOTAL NEMATODES	80	44.2	452	5.65	1-35	0.50	0-2
C. anatis	78	43.1	430	5.15	1-35		
P. crassum	8	4.4	12	1.50	1-3		
T. tenuis	1	0.5	4	4	4		
TOTAL HELMINTHS	177	97.8	8218	46.44	1-473	3.17	0-9

C. megalops may reflect competition for space in the species' rather confined habitat. *Fimbriaria fasciolaris* too was relatively common, and although this species occurred in fewer birds, burdens were often larger than found for *C. megalops*. The greatest number of *F. fasciolaris* found in any bird collected in May was 52, though 76 were found in the intestine of a young duck collected in December.

The two other cestode species found during the study were not present in May. They were only found in young birds during late spring and early summer and even then were comparatively rare occurrences.

Only one species of nematode - *C. anatis* - occurred frequently in the lower alimentary tract of *T. variegata*. Nearly half of the birds were infected with this species (Table 6), but infections were rarely large. The average number per infected bird in May was only 5.5, although numbers ranged up to 35 and 131 were recorded from one young bird during December. *Porrocaecum crassum* was found often enough for it to be recognised as a normal parasite of *T. variegata*. Eight of the birds in the May samples were infected with the species and numbers ranged up to three. The highest number recorded in a single infection was 12, which were in a young bird taken in December.

III. COMPARISONS BETWEEN ADULT/JUVENILE AND MALE/FEMALE INFECTIONS

Of the 281 shelducks in the total sample 135 were juveniles and 146 were adults, and 142 were females and 139 were males.

Differences in parasite loads between males and females and different age classes are frequently found in many host species. Such differences have been discussed by Dobson (1962) with regard to rodents, Owen and Pemberton (1962) for starlings, Threlfall (1967) for gulls, and Cornwall and Cowan (1963) for the Canvasback Duck.

To see if any such differences occur in Paradise Shelducks, incidences and intensities of infection were compared between juveniles and adults, and males and females. In cases where there appeared to be some

Table 7. COMPARISON OF INFECTIONS OF LOWER GASTRO-INTESTINAL TRACTS OF ADULTS AND JUVENILES

(A) NOVEMBER-JANUARY

	JUVENILE (5)					ADULTS (25)				
	number infected	% incidence	total no. parasites	mean intensity	mean diversity	number infected	% incidence	total no. parasites	mean intensity	mean diversity
TOTAL CESTODES	5	100	132	26.4	2.2	18	72	70	3.9	0.8
C. megalops	2	40	7	3.5		15	60	61	4.1	
F. fasciolaris	5	100	99	19.8		5	20	8	1.6	
A. furcigera	2	40	16	8.0		-	-	-	-	
S. gracilis	1	20	1	1.0		-	-	-	-	
A. ciliata	1	20	9	9.0		1	4	1	1.0	
TOTAL TREMATODES	5	100	914	182.8	2.8	17	68	298.2	175.4	0.8
U. gippyensis	3	60	139	49.7		-	-	-	-	
N. attenuatus	1	20	9	9.0		2	8	37	18.5	
N. tadornae	4	80	307	76.8		7	28	2759	394.1	
H. conoideum	1	20	58	58.0		-	-	-	-	
Echinostoma sp.	1	20	1	1.0		-	-	-	-	
E. revolutum	-	-	-	-		-	-	-	-	
E. recurvatum	3	60	399	133.0		7	28	178	25.4	
C. cornutus	1	20	1	1.0		3	12	8	2.7	
TOTAL NEMATODES	3	60	151	50.3	1.4	12	48	42	3.5	0.5
C. anatis	3	60	131	43.7		11	44	37	3.4	
P. crassum	3	60	19	6.3		2	8	5	2.5	
T. tenuis	1	20	1	1.0		-	-	-	-	
TOTAL HELMINTHS	5	100	1197	239.4	6.4	23	92	3094	134.5	2.1

Intensity = number of individuals per infected bird; Diversity = number of species per bird

Table 7 (continued)

(B) MAY

	JUVENILE (109)					ADULT (72)				
	number infected	% inci-dence	total no. parasites	mean intensity	mean diversity	number infected	% inci-dence	total no. parasites	mean intensity	mean diversity
TOTAL CESTODES	79	72.5	480	6.08	0.96	59	81.9	312	5.29	1.14
C. megalops	54	49.5	235	4.35		57	79.2	205	3.60	
F. fasciolaris	51	46.8	245	4.80		25	34.7	107	4.28	
A. furcigera	-	-	-	-		-	-	-	-	
S. gracilis	-	-	-	-		-	-	-	-	
A. ciliata	-	-	-	-		-	-	-	-	
TOTAL TREMATODES	105	96.3	3984	37.94	1.95	53	73.6	2990	56.42	1.15
U. gippyensis	87	79.8	456	5.24		2	2.8	2	1.00	
N. attenuatus	-	-	-	-		1	1.4	160	160.00	
N. tadornae	81	74.3	3415	42.16		42	58.3	2506	59.67	
H. conoideum	-	-	-	-		-	-	-	-	
Echinostoma sp.	1	0.9	3	3.00		-	-	-	-	
E. revolutum	16	14.7	31	1.94		2	2.8	2	1.80	
E. recurvatum	11	10.1	4.8	4.36		14	19.4	272	19.43	
C. cornutus	17	15.6	31	1.82		22	30.6	48	2.18	
TOTAL NEMATODES	50	45.9	338	6.76	0.54	29	40.3	112	3.86	0.43
C. anatis	50	45.9	322	6.44		28	38.9	108	3.86	
P. crassum	6	5.5	10	1.67		2	2.8	2	1.00	
T. tenuis	3	2.8	6	2.00		-	-	-	-	
TOTAL HELMINTHS	108	99.1	4802	44.46	3.46	69	95.8	3414	49.48	2.72

Intensity = number of individuals per infected bird; Diversity = number of species per bird likelihood that differences were not merely due to chance, Chi^2 tests using 2 x 2 contingency tables were applied to the incidence data, while Kruskal-Wallis non-parametric tests (Sokal and Rohlf, 1966) were used to check the significance of differences found in intensity data. The Kruskal-Wallis test does not test the difference between means as does the t-test, but rather differences in distribution of data. For this reason it proved particularly useful for testing the intensity data, as the occasional exceptionally large infection of a host by a particular species - which influenced means considerably - did not influence the results of the test to such a great extent.

The number of parasite species infecting a host indicates the diversity of the infection. This measurement is a convenient one to compare infections by cestodes, trematodes, nematodes and helminths as groups. The diversity data was also tested using Kruskal-Wallis tests.

1) Comparison of Adult/Juvenile Infections

Of the 22 helminth species recovered from *T. variegata* during the study 16 were found infecting adult birds, while 18 were recovered from juveniles. Six species found only in juveniles were *Hypoderaeum conoideum, Echinostoma* sp, *Aploparaksis furcigera, Trichostrongylus tenuis, Typhlocoelum* sp. and *Sobolevicanthus gracilis*. While *Tetrameres* sp., *Dendritobilharzia pulverulenta, Epomidiostomum uncinatum* and *Syngamus* sp. were found only in adults.

Only five juvenile birds (progeny of the 1972-1973 breeding season), were obtained during November 1972 to January 1973 inclusive. Nevertheless, they appeared to be more heavily parasitised than adult birds taken in the same period. They averaged 6.4 intestinal helminth species per bird (S.D. - 1.50), while adult birds recovered in this time averaged only 2.1 species per bird (S.D. - 1.34). The higher figure seen for the younger birds at this time of the year, was apparently partly due to their possession of species which were rarely if ever found in the adult shelducks. The species concerned were *H. conoideum, Echinostoma* sp., *T. tenuis, N. attenuatus, A furcigera, S. gracilis* and *A. ciliata*. In addition, two specimens of *Typhlocoelum* sp. were found in the air-sacs of one of these birds, this being the only record of this species from the shelduck throughout the study.

Table 7 compares the helminth invasions of juvenile and adult birds taken between November 1972 and January 1973. The raw data for these birds is shown in Appendix 3. For the purposes of this comparison, one bird which still possessed the remnants of a bursa of Fabricius - and so was probably one of the progeny of the previous breeding season - is included as an adult. Though the samples are small, it is clear from this table (and from Appendix 3), that not only do the juvenile shelducks possess a greater range of helminths of all the major groups, but also in general they are infected with noticeably larger burdens. The exceptionally large mean for trematodes infecting adult birds is due to the presence in the January sample of three birds with large infections of *N. tadornae*. The reason for these infections is discussed in Section IV.

By May "juvenile" shelducks are already 6-7 months old, but as they still possess bursae at this stage they are considered juvenile birds. However, by this age it could be expected that their parasite fauna would resemble that of adult birds more closely than that of non-flying birds one to two months old (such as those considered above). Table 7 shows incidences and intensities of infections by helminths in both adult and juvenile shelducks in May 1971, 1972 and 1973. As expected differences between adult and juvenile birds in these data are in general not so obvious. However, the sample is large enough to allow statistical testing where necessary. From the table it can be seen that incidences of infection by helminths as a whole do not appear to differ significantly between juveniles and adults. Nevertheless, some highly significant differences are present at lower levels. For example, trematodes infected 96.3% of juveniles in the May samples, while only 73.6% of adults were infected by species of this group ($X^2 = 20.18$, $p < 0.001$). No differences are apparent for the incidence of cestodes or nematodes. Similarly, though diversities of cestode and nematode infections in adults and juveniles do not appear to differ significantly, it was found that adults were infected with a mean of 1.15 species of trematodes, while juveniles in the sample possessed a mean of 1.95 species ($H = 27.9$, $p < 0.001$). The differences seen are due to large differences in infection at the species level.

The largest difference in infection of juveniles and adults at the species level is seen for *U. gippyensis*. Almost 80% of juveniles in the May samples were infected with this species, while only two adults (representing 2.8% of the adults in the sample) were infected each with a single specimen. The average number of *U. gippyensis* infecting young birds was 5.24. Such large differences need no testing for significance. The differences in *U. gippyensis* infections of adults and juveniles are simply explained. The usual habitat of *U. gippyensis* is within the bursa of Fabricius of the host - an organ which is present only in juvenile birds. The entrance to the bursa lies in a small pocket in the wall of the cloaca, and this pocket remains in adult birds. It is possible that this pocket could provide a habitat of marginal quality for *U. gippyensis*. This could account for the presence of this species in the cloacas of a small proportion of young birds and could also explain how infection of adults is possible. From their size it appears certain that the four specimens of *U. gippyensis* which were present in adults, were resident in these birds.

Notocotylus tadornae and *E. revolutum* also both infect a significantly higher proportion of juveniles than adults. *Notocotylus tadornae* occurred in 74.3% of juveniles and 58.3% of adults ($X^2 = 5.09$, $p < 0.025$) and *E. revolutum* was found infecting 14.7% of juveniles but only 2.8% of adults ($X^2 = 6.86$, $p < 0.01$). The differences here may be due to a lack of immunity in young birds, as differences in food or behaviour cannot account for them (see Chapter 3).

It has already been pointed out earlier in this section that several helminth species which were rarely found during the study, were recovered from juvenile shelducks. During May, two species - *T. tenuis* and

Echinostoma sp. - were found in juveniles only.

Infections of unusual size were also usually found in juveniles rather than adults. Of the regular parasites of *T. variegata* the largest infections of *C. megalops, F. fasciolaris, U. gippyensis, E. recurvatum, E. revolutum, C. anatis* and *P. crassum* were all recorded from juvenile birds.

Differences found in infections of adults and juveniles by other species of helminths are more puzzling. *Cloacotaenia megalops* and *Cotylurus cornutus* both infected a significantly higher proportion of adults than juveniles, even though the intensities of their infections in the two age classes were similar. As Table 6 shows, *C. megalops* occurred in 79.2% of adult shelducks in May, as opposed to only 49.5% of juveniles ($X^2 = 16.18$, $p < 0.001$), and *C. cornutus* was found in 30.6% of adults and only 15.6% of juveniles ($X^2 = 5.74$, $p < 0.02$). A possible explanation in the case of *C. megalops* is a trap and accumulation effect. Buscher (1965) expressed a belief that *C. megalops* is a long-lived species. If this is the case a higher percentage of birds over one year old is likely to be infected than those of less than one year. The fact that intensities of infection are similar for both age groups may be due to competition for space in the species confined habitat. *Cotylurus* spp. on the other hand are generally considered to be relatively short-lived, about seven days in the final host for *C. flabelliformes* and 7-16 days for *C. brevis* (McDonald, 1969) - and so no similar explanation is possible for *C. cornutus*.

Echinoparyphium recurvatum was also found infecting about twice as many adults as juveniles (19.4% of adults, 10.0% of juveniles), though this is not quite significant at the 5% level of confidence. With a larger sample size this may have proved significant. There is a great similarity between the life histories and habitats of *E. recurvatum* and *C. cornutus*. If the difference in infections of adult and juvenile shelducks seen for *E. recurvatum* is a real one, then the causal factor is probably the same as that which is responsible for the difference seen for *C. cornutus*. This may simply be due to differences in habitat utilisation by adults and juveniles (discussed in Chapter

Table 8. COMPARISON OF INFECTIONS OF LOWER GASTRO-INTESTINAL TRACTS OF MALES AND FEMALES IN MAY

	MALE (89)					FEMALE (92)				
	number infected	% incidence	total no. parasites	mean no./ infected bird	mean no. spp./bird	number infected	% incidence	total no. parasites	mean no./ infected bird	mean no. spp./bird
TOTAL CESTODES	67	75.3	440	6.57	1.03	71	77.2	352	4.96	1.03
C. megalops	57	64.0	232	4.07		54	58.7	208	3.85	
F. fasciolaris	35	39.3	208	5.94		41	44.6	144	3.51	
TOTAL TREMATODES	76	85.4	3642	47.92	1.62	82	89.1	3332	40.63	1.65
U. gippyensis	46	51.7	300	6.52		43	46.7	158	3.67	
N. tadornae	61	68.5	2881	47.23		62	67.4	3040	49.03	
E. revolutum	7	7.9	10	1.43		11	12.0	23	2.09	
E. recurvatum	15	16.9	255	17.00		10	10.9	65	6.50	
C. cornutus	14	15.7	36	2.57		25	27.2	43	1.72	
TOTAL NEMATODES	42	47.2	258	6.14	0.52	37	40.2	192	5.19	0.46
C. anatis	41	46.1	245	5.98		37	40.2	185	5.00	
P. crassum	5	5.6	7	1.40		3	3.3	5	1.67	
TOTAL HELMINTHS	87	97.8	4340	49.89	3.19	90	97.8	3876	43.07	3.14

III). The situation seen for *C. megalops* may also be explained as simply as this.

2) Comparison of Male/Female Infections

Table 8 shows incidences and intensities of infections of male and female shelducks for the May sample. A comparison of these figures indicates that infections by helminths, cestodes, trematodes and nematodes at the group level are very similar for both sexes. However, at the species level a difference for one species is seen. The average intensity of infections by *U. gippyensis* is much greater in males than in females (although the incidence is similar in both sexes). Males possessed a mean of 6.52 *U. gippyensis* per infected bird while females were on the average infected with only 3.67 ($H = 16.35$, $p < 0.005$). Such a difference is not seen for *N. tadornae* despite having the same intermediate host species and similar encysting habits as *U. gippyensis* (see Chapter V). This probably indicates that the difference in intensity of *U. gippyensis* infections between males and females does not merely reflect differences in diet between the sexes. Hormonal or morphological differences may be responsible.

None of the other apparent differences in infections of males and females proved significantly different.

IV. SEASONAL CHANGES IN INFECTION OF *T. VARIEGATA*

As mentioned in Chapter II, there are marked seasonal climatic changes in the study area. While these changes are not of the same order as those which cause the migration of many waterfowl species in the Northern Hemisphere, they still affect the ecology of both the definitive and intermediate hosts. Consequently, the dynamics of the helminth fauna in *T. variegata* could be expected to be influenced to some extent.

The monthly samples of Paradise Shelduck from the main study area were examined to investigate the seasonal dynamics of the helminth fauna. Because some differences in levels of infection exist between juveniles and adults, to effectively understand the situation in the overall population, the proportions of juveniles and adults in the monthly samples should ideally reflect the proportion in the population at the time of sampling. Although it was not possible to do this very accurately, the proportions of juveniles and adults in the monthly samples nevertheless approximate those of the birds seen on collecting trips. It is therefore considered valid to combine data from the juvenile and adult birds to represent seasonal abundance of parasites of the shelducks in the study area. The low proportion of juveniles during and after the 1972-1973 breeding season reflects the relatively poor breeding success in the vicinity during that season. Very few broods appeared to have been raised, even in areas unaffected by sampling.

The intensity of invasion of shelducks by helminths is extremely variable from one bird to another. Thus, particularly when using small samples, the intensity data tends to fluctuate a great deal. Data for the incidence of invasions are more useful to give an indication of seasonal changes in helminth infections. However, the incidence data too, are susceptible to some variation when samples are small (although not to the same extent as for intensity). Fluctuations in the data are in many cases associated with the impossibility of exact replication of monthly samples. Although the monthly samples of shelducks used to provide data for this section were always collected in the same general area so as to minimize variation caused by location, there are many microhabitats throughout the study area occupied by the shelducks. Considering this and the fact that adult shelducks are strongly territorial for much of the year, it is understandable that often the birds vary widely in the parasite loads that they carry. Only by using much larger monthly samples could fluctuations have been reduced in the monthly data. Thus, to deal effectively with the data obtained from relatively small samples, some arranging on a bi-monthly basis was necessary. Fig. 33 shows graphs derived from the monthly incidence data in Table 9. In an attempt to dampen fluctuations in the monthly data yet avoid concealment of any information by grouping data, these graphs show monthly incidence values as points but the graphline passes through points based on bi-monthly incidence values.

Table 9. MONTHLY FLUCTUATIONS IN INCIDENCE (I) AND DIVERSITY (D) OF INFECTIONS BY MAJOR HELMINTH GROUPS

		May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	May
Cestodes	I	9	8	8	7	6	7	9	7	7	9	9	9
	D	1.0	1.2	1.1	1.0	0.9	1.2	1.5	0.9	0.8	1.0	1.3	1.1
Trematodes	I	10	10	8	9	7	8	9	7	6	5	9	8
	D	1.7	1.8	1.2	1.9	0.9	1.0	1.1	1.4	0.8	0.6	1.5	1.4
Nematodes	I	8	8	5	5	6	3	5	7	5	4	4	6
	D	0.8	0.8	0.5	0.5	0.6	0.3	0.5	1.0	0.7	0.4	0.4	0.6
All helminths	I	10	10	10	9	10	9	9	9	10	9	10	10
	D	3.5	3.8	2.8	3.4	2.4	2.5	3.1	3.3	2.3	2.0	3.2	3.1

1) Seasonal Changes in *T. variegata*'s Helminth Load

The occurrence of helminths in the lower alimentary tract of the Paradise Shelduck is high throughout the year, but there is a noticeable drop during the spring and summer months of the sampling period (Fig. 33i and Table 9). The incidence did not drop dramatically, but, because the data for total helminth infection is so consistently high, this drop during the spring and summer does appear to reflect a similar drop throughout the population. Separate analyses of adult and juvenile incidences (Table 10), indicate that a lowering of incidence in adult birds only is responsible for the change in overall incidence seen in Fig. 33i. At no time during the study was a completely uninfected juvenile bird found.

The diversity of the helminth fauna infecting a bird is indicated by the number of helminth species present simultaneously. The mean number of helminth species per bird in each monthly sample gradually declined throughout the winter from a peak in autumn (3.8), until September when 2.4 helminths were present per bird in the sample. The number then rose again to form a second peak during

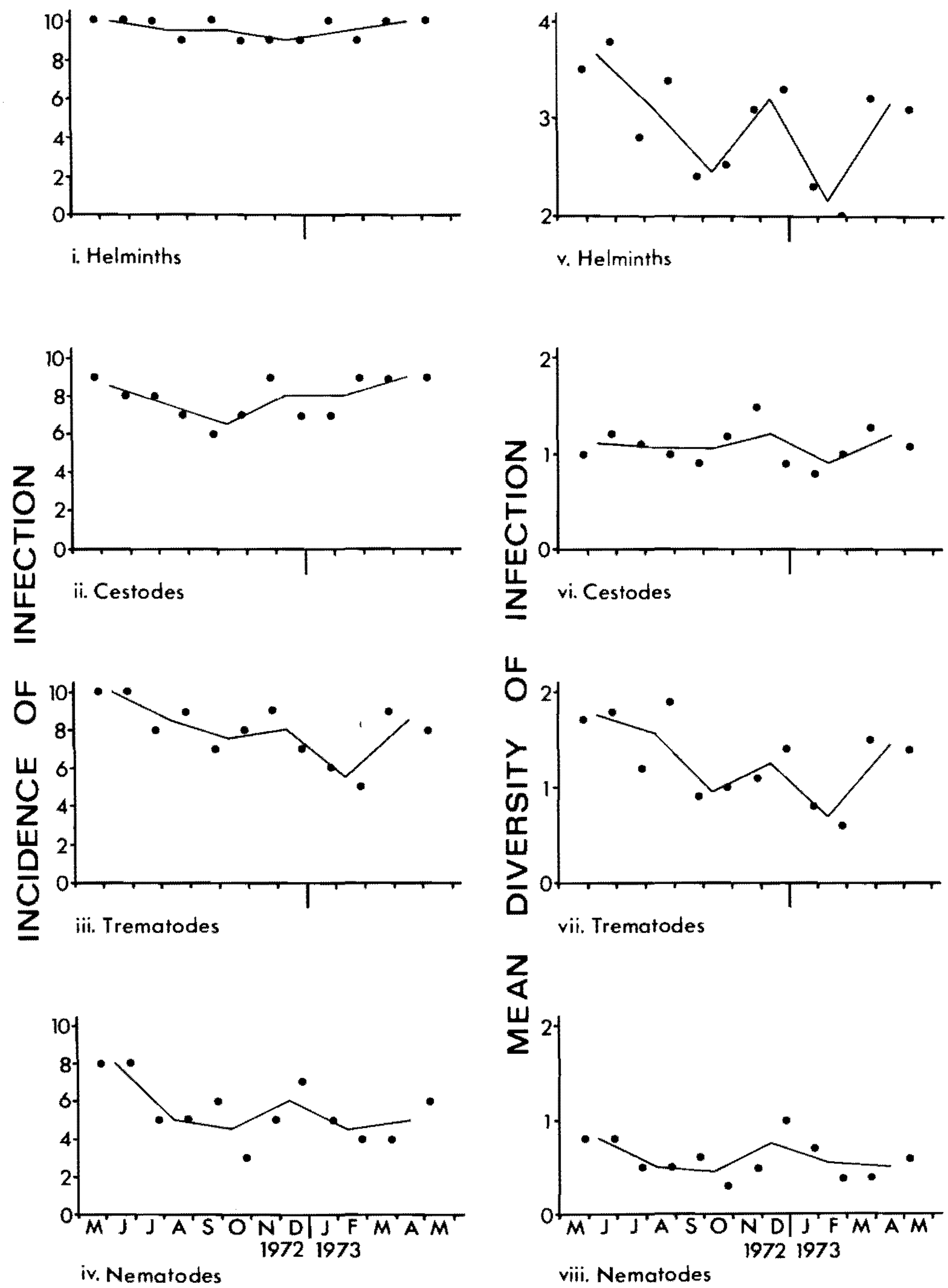


Figure 33. Monthly fluctuations in incidence and diversity of infections by major helminth groups.

the summer (Fig. 33v). As for the monthly incidence data, adult birds were not responsible for the high level of diversity seen during the summer. Table 10 gives the levels of diversity of helminths of adult and juvenile shelducks throughout the year. From these values it can be seen that diversity of helminths in the adult birds fell away fairly constantly until its lowest level in January (mid summer), when 1.7 helminth species per adult bird were found. Diversity in juveniles on the other hand, fell away only until late September (by which stage juveniles are nearly one year old). It then rose sharply with the influx of new ducklings into the population, and builds up to form a peak of eight helminth species per bird in January.

Table 10. MONTHLY CHANGES IN INCIDENCE AND DIVERSITY OF HELMINTHS IN ADULT AND JUVENILE SHELDUCKS

	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	May
No. juveniles in sample	6	4	3	2	6	5	2	2	1	1	0	3
% incidence	100	100	100	100	100	100	100	100	100	100	?	100
Diversity	3.3	4.3	3.7	3.5	2.3	2.8	5.0	7.0	8.0	3.0	?	4.0
No. adults in sample	4	6	7	8	4	5	8	8	9	9	10	7
% incidence	100	100	100	87	100	80	87	87	100	89	100	100
Diversity	3.7	3.5	2.4	3.4	2.5	2.2	2.6	2.4	1.7	1.9	3.2	2.7

The suggestion of two peaks in the level of helminth infection (autumn and summer) is strengthened by the similarity of patterns seen for both diversity and incidence of infections of all three major helminth groups found infecting shelducks (Fig. 33). Rind (1974) reported two peaks in levels of infection for Grey and Mallard Ducks in New Zealand, but these were in summer and autumn. The autumn peak found by Rind probably corresponds to that found in the present study, while her August peak is much earlier than the summer one seen for high country shelducks, and is probably caused by a different set of factors.

The observed patterns of incidence and diversity in the shelducks can be explained fairly simply in the light of what has already been discussed in previous chapters:

a) The numbers of helminths infecting the shelducks decline slowly throughout the winter months possibly due to dying off of intermediate hosts, a simultaneous reduction in their accessibility to shelducks (due to surface ice and migration down the water column of surviving invertebrates), and a reduction in the rate at which infective larvae are released from their intermediate hosts at lower temperatures. Thus both intensity and diversity of parasites fall away simultaneously. The incidence of helminth infections remains high longer, possibly due partly to the presence of long-lived species and partly to the reduced number of new infections which still take place. The acquisition of immunity may also play a part in reducing numbers of helminths at this time, particularly in the young birds.

b) About mid-spring (October), the first of the season's ducklings begin to enter the population. They appear to have less resistance to infection than adult shelducks, and probably like most young birds, require a more highly proteinaceous diet than their parents. Thus, at first they probably rely little on grazing and may eat large numbers of aquatic invertebrates, while adults particularly those without broods are grazing on terrestrial plants. The number of helminth species per bird in the population rises rapidly at this time due to large infections in the new season's young birds. Because young shelducks tend to be restricted in mobility, the species of parasites they carry and the intensities of infections, vary considerably with the ducklings' microhabitat. The helminth burdens of the young birds increase in size with age, due partly to time alone but possibly also to a second generation of helminths in the restricted feeding grounds. Dietary factors - particularly the onset of the berry season - coupled with a greater resistance to infection, may account for the lack of a simultaneous rise in infection levels of adults in early summer.

c) By mid summer (January) most of the season's young shelducks are mobile and no longer feeding in such restricted and sheltered areas. The likelihood of more new infections is thus reduced and young birds have probably acquired a degree of immunity to reinfection and thus by February the number of helminth species per young bird decreases to some extent. At the same time the infections in adults slowly increase in size once more due to a build up in numbers of infected intermediate hosts. Thus, the incidence and diversity of helminths in the overall population rises towards the autumn level once more.

2) Seasonal Abundance of the Commoner Helminth Species

Three of the helminth species found in the lower alimentary tracts of Paradise Shelducks appeared only during mid-spring to mid-summer. These species - *A. fürcigera, H. conoideum* and *S. gracilis* - have been mentioned previously as having been restricted to non or newly flying juveniles. Five more species - *N. attenuatus, Echinostoma* sp., *E. revolutum, P. crassum* and *A. ciliata* were found infrequently throughout the year, but except for *E. revolutum* they were also most commonly encountered during the spring and early summer. *Echinostoma revolutum* was found mainly in autumn. These species were all most commonly (but not invariably) in juveniles.

The remaining species from the lower tracts were found more often. From a comparison of monthly incidences (Table 11), it is obvious that some of the species undergo changes in levels of infection throughout the year. It is likely that some of these changes are cyclic, though another year's sampling would be needed before this could be stated with any degree of certainty.

The incidence of *C. megalops* was highest in autumn and fell away to its lowest level by mid summer (December) (see Fig. 34). Similarly both common species of notocotylid occurred at their highest levels in autumn. The incidence of *N. tadornae* reached its lowest level in December - only two of the 10 shelducks in that month's sample were infected - and *U. gippyensis* was least common in early spring

Table 11. MONTHLY FLUCTUATIONS IN INCIDENCE AND INTENSITY OF THE COMMONER HELMINTH SPECIES

		May	June	July	August	September	October	November	December	January	February	March	May
No. juveniles in sample		6	4	3	2	6	5	3	2	1	1	0	3
C. megalops	incidence	9	6	8	6	6	6	7	4	6	6	8	9
	intensity	3.2	2.0	4.5	4.2	3.3	2.5	4.1	2.0	5.2	2.8	4.1	3.8
F. fasciolaris	incidence	1	6	3	4	2	5	4	4	2	4	5	2
	intensity	1.0	3.0	5.7	5.3	1.5	1.2	4.0	22.0	1.5	4.3	17.0	2.0
*U. gippyensis**	incidence	83%	100%	100%	100%	33%	20%	67%	50%	0%	100%	?	100%
	intensity	4.0	2.8	2.3	1.3	2.5	1.0	4.0	131.0	0.0	26.0	?	5.0
N. tadornae	incidence	10	10	7	6	5	8	5	2	4	3	8	6
	intensity	57.7	349.8	53.3	82.0	19.6	33.9	79.0	45.0	645.3	52.3	120.4	36.0
E. recurvatum	incidence	2	2	1	4	0	0	1	7	2	2	2	2
	intensity	2.0	23.5	4.0	5.0	0	0	6.0	61.1	71.5	6.5	16.0	3.0
C. cornutus	incidence	0	2	1	5	2	1	3	1	0	0	3	2
	intensity	0	2.5	5.0	1.8	3.5	7.0	2.7	1.0	0	0	1.7	3.0
C. anatis	incidence	8	8	5	5	6	3	3	6	5	4	4	6
	intensity	6.0	4.3	5.2	2.0	2.0	2.3	2.3	22.5	5.2	2.0	2.5	2.5

Incidence = number of birds in monthly sample infected; Intensity = mean number per infected bird

* Incidence of *U. gippyensis* refers to juveniles in the samples only, as it would otherwise simply reflect proportion of juveniles present.

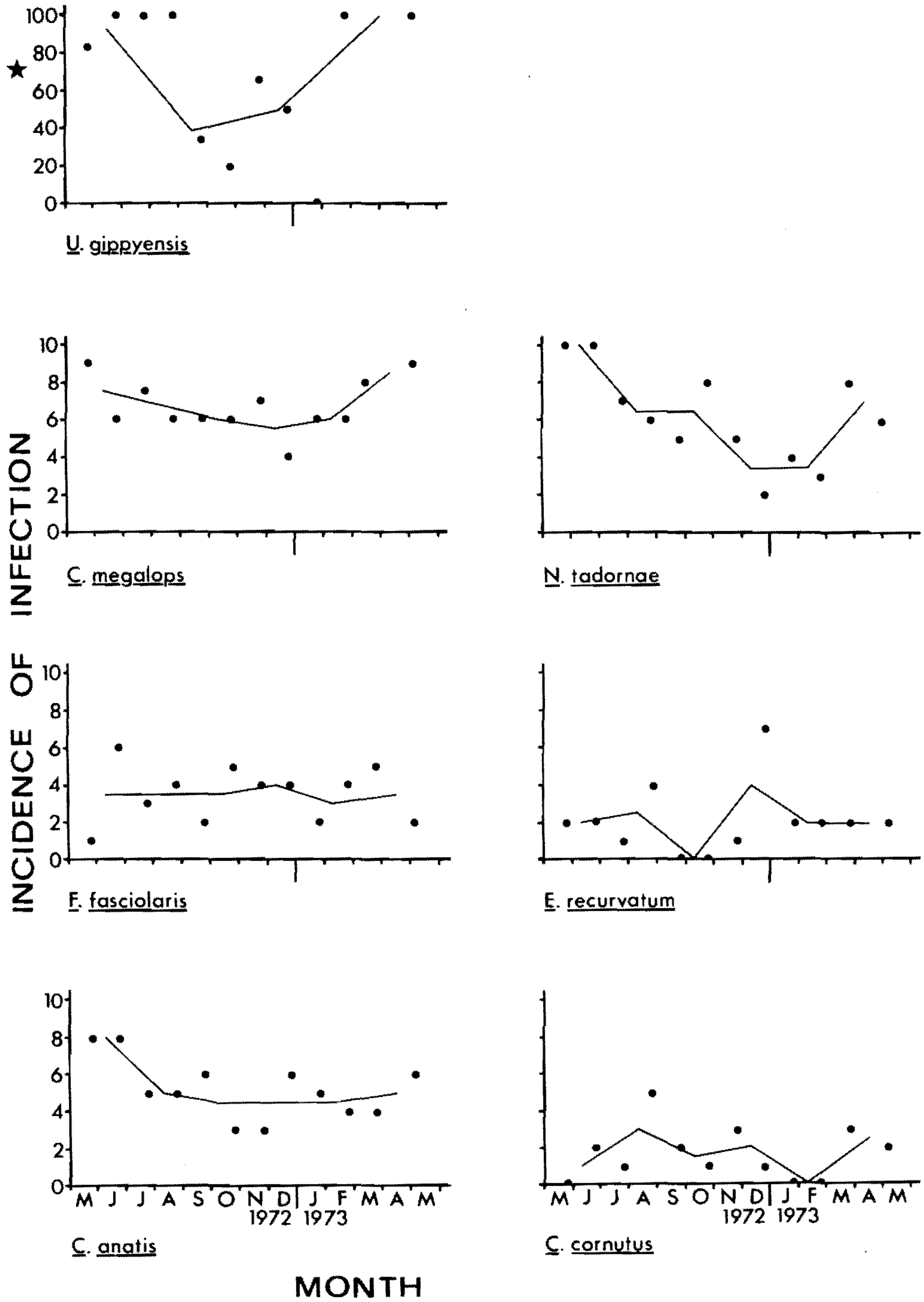


Figure 34. Monthly fluctuations in incidence of the commoner helminth species.

* Incidence of *U. gippyensis* refers to juveniles in the sample only.

just before the large influx of new broods of ducklings. It is important to note that values for incidence of *U. gippyensis* are derived from juveniles in the samples only. Numbers of juveniles in the samples from November on are very low, and so to allow comparison of the seasonal abundance of *U. gippyensis* with other species, it was necessary to arrange the data on a quarterly basis. Even with this treatment the numbers of juveniles in each group are small. However, it is possible to see a trend which is probably cyclic (Fig. 34).

Although incidence of *F. fasciolaris* fluctuated considerably throughout the monthly samples, the graphline through the bi-monthly points indicates a fairly constant level of infection throughout the year.

Data for incidence of *E. recurvatum, C. cornutus* and *C. anatis* are more difficult to interpret without further information. Seasonal patterns of abundance are less obvious. However, if an apparent rise in incidence of *E. recurvatum* in August is assumed to be caused by factors other than the time of year (e.g. the sampling locality), then it can be seen that this species follows a similar pattern of abundance to those seen for *C. megalops* and the notocotylid trematodes - a lowering of abundance from autumn towards spring then a rise again over the summer. The high incidence seen for *E. recurvatum* in December is probably also a local effect as the December sample was taken from the Magdalene Valley (a valley which contains much more swampland than was found in other valleys of the sampling area). Three shelducks flushed from these swamps were found to contain very large burdens of *E. recurvatum*. Most of the other ducks in the December sample must also have had easy access to such swamps. Strangely the incidence of *C. cornutus* in December does not follow that of *E. recurvatum* as closely as it might have been expected to do considering that these two species are reported to use the same intermediate hosts. However, similarities can be seen in the timing of the fluctuations of incidence, particularly during the first half of the sampling period.

It has been pointed out earlier in this section that the intensity data from such small monthly samples is unsuitable for investigating seasonal dynamics. Nevertheless, seasonal intensity data has been included in Table 11 as they provide other interesting information. The intensity data show some large fluctuations for which no correspondingly large fluctuations are seen in incidence levels. Many of these are due to unusually large individual burdens of various helminth species, rather than the result of a general trend in the data of that sample. Generally when a large burden of any species of helminth builds up in a bird it is because that bird continually inhabits an area in which a particular intermediate host species is numerous. This often happens in the case of Paradise Shelducks during the breeding season and the moult, when the feeding activities of these birds are confined to smaller areas than usual. December and January stand out quite noticeably as the two months involved. Young shelducks during the breeding season are often confined to a limited feeding area until they can fly. This is especially so if they are raised on a small pond or swamp (as opposed to a riverbed where movement is less restricted). The two young shelducks collected in December from different swamps in the study area were responsible for the unusually high mean intensities of *U. gippyensis, F. fasciolaris, E. recurvatum* and *C. anatis* recorded in this month. The duck with the large burden of *U. gippyensis* was taken from an area of swamp through which flowing water passed. Large numbers of the snail *Potamopyrgus antipodarum* inhabited the area. The bird with unusually large numbers of *F. fasciolaris, E. recurvatum* and *C. anatis* was obtained from a swamp whose water was still and partially stagnant. Large numbers of a variety of aquatic invertebrates, including the snails *Lymnea tomentosa* and *Gyraulus corinna,* were present. No *P. antipodarum* were present and it was noted that this duck contained no *U. gippyensis.* Another young duck taken from the same swamp during the following month (January), also had a particularly large burden of *E. recurvatum,* causing a similarly high mean intensity of this species to be seen for the January sample.

Although only young birds have been mentioned here with regard to having large loads of various helminth species during the breeding season, it may be that their parents also possess larger loads of some species than usual (no adult birds with broods were collected). This would probably apply more particularly to the female, which spends more time feeding with the brood, than the male which is often stationed at a distance acting as a sentry.

The moulting of adult Paradise Shelducks is discussed in Chapter II. Three birds in mid-moult were obtained during January from a mob of approximately 300 birds moulting on one of the lakes in the study area. This lake contained a particularly high density of *P. antipodarum* and the birds from here all contained large numbers of *N. tadornae*.

It is apparent from these examples that during breeding and moulting, burdens of unusual size are often present, but that types and diversity of helminths present in such burdens depend largely on the type of habitat the shelduck is occupying at the time.

V. DISCUSSION

Nearly all previous studies involving seasonal abundance of helminths in waterfowl have been carried out on migratory species, and so are not directly comparable with this study. Helminth infections of migratory species of waterfowl in Europe and North America are typically at a maximum during the summer (at the nesting grounds) and there is a decrease through autumn (during migration) to the lowest level in winter (Buscher, 1965; Bezubik, 1956; Avery, 1966a).

After studying several migratory species of waterfowl in North America, Buscher (1965) postulated that the reduction of helminth fauna during autumn was probably the result of several factors including: 1) a loss due to unfavourable conditions of migration; 2) a loss of naturally short-lived forms during migration; and 3) reduced chances of new infections during and after migration.

The stresses placed upon the helminth fauna of migrating birds are probably much greater than for non-migratory host species. Thus it could be expected that the helminths of migratory species are subject to greater seasonal variations. The loss of short-lived helminth species is constantly taking place whether the host is migratory or not, but it is likely that the migrating host will be exposed to a different group of intermediate hosts in its wintering grounds than were present in its breeding grounds. These short-lived forms are therefore less likely to be replaced in migratory hosts. For a non-migratory species this situation does not arise. Even so, it appears that chances of new infections taking place are still reduced to some extent during the winter due to the effects of harsher climatic conditions on intermediate host species.

In a recent North American study Kinsella and Forrester (1972) showed that the cestodes and trematodes of the Florida Duck (*Anas platyrhynchos fulvigula*), a non-migratory race of Mallard, increased in prevalence through the summer months to reach peaks in November (autumn), and then fell off to their lowest points in February and March (late winter and early spring). The genera *Cloacotaenia, Echinostoma* and *Echinoparyphium* are specifically mentioned in this regard. This approximates the situation seen in the present study for most of the commoner helminth species of *T. variegata*. Climatic differences between Florida and the Canterbury high-country possibly account for the slightly later rise in incidence of helminths observed in *T. variegata*.

CHAPTER VII

COMPARISON OF THE PARADISE SHELDUCK WITH OTHER WATERFOWL SPECIES

I. OTHER WATERFOWL SPECIES FROM THE STUDY AREA

A comparison between aspects of the ecology and the helminth faunae of different waterfowl species, can help give a better understanding of the relationships between parasites and the ecology of their hosts. Accordingly, such a comparison was carried out on a small scale for the study area.

As mentioned in Chapter II, four other species of waterfowl were seen in the study area during the sampling period. Of these, six Grey Ducks, one Mallard and two Canada Geese were collected during the shooting seasons of 1972, 1973 and 1974. They were examined for food species and helminth parasites in the same manner as used for the Paradise Shelducks. As the koilin lining of the gizzard of the Mallard and Grey Ducks was easy to remove, it was possible to conduct a quantitative examination of the gizzard helminths.

1) Diets

Food species found from the Mallard, Grey Ducks and Canada Geese are listed in Table 12, with the frequencies of their occurrences. From this table it can be seen that the diet of the "dabbling species" (Mallard and Grey Ducks), is quite different from that of Paradise Shelducks. While the shelducks are basically grazing birds, the Mallard and Grey Ducks examined contained no terrestrial leaf material at all. Seeds and berries of terrestrial plants were reasonably common - particularly those of sweet briar, *Lilaeopis* sp. *Coprosma* spp. and sedges. It should be recognised however, that because seeds are hard (particularly those of sweet briar), they tend to remain in the gizzard for considerably greater lengths of time than most other foods. Thus their importance as food items is easily overestimated. Nevertheless, frequencies are directly comparable with those in Paradise Shelducks as the same

Table 12. FOOD SPECIES FROM THE TRACTS OF MALLARDS, GREY DUCKS AND CANADA GEESE FROM THE STUDY AREA.

MALLARD AND GREY DUCKS (7)		Frequency of Occurrence
TERRESTRIAL PLANTS - SEEDS & BERRIES		5
DICOTYLEDONES		
Leguminosae	*Trifolium repens*	1
Rosaceae	*Rosa rubiginosa*	4
Rubiaceae	*Coprosma* spp.	3
Umbeliferaceae	*Lilaeopsis* sp.	3
MONOCOTYLEDONES		
Cyperaceae	*Scirpus* sp.	2
	Carex sp.	1
	gen. undet.	2
AQUATIC PLANTS - VEGETATIVE		3
DICOTYLEDONES		
Ranunculaceae	*Ranunculus fluitans*	2
Lemnaceae	*Lemna* sp.	1
	Aquatic debris	1
AQUATIC PLANTS - SEEDS		
DICOTYLEDONES		
Ranunculaceae	*Ranunculus* sp.	1
Potamogetonaceae	*Potamogeton cheesemani*	2
AQUATIC ANIMAL MATERIAL		6
MOLLUSCA		
Hydrobiidae	*Potamopyrgus antipodarum*	5
Planorbidae	*Gyraulus corinna*	1
CRUSTACEA		
S.C. Copepoda		
O. Cyclopoidea	gen. undet.	1

Table 12 (continued)

		Frequency of Occurrence
INSECTA		
O. Diptera	(larva) gen. undet.	
O. Trichoptera		
Sericostomatidae	*Pycnocentrodes aureola*	1
CANADA GEESE (2)		
TERRESTRIAL PLANTS - VEGETATIVE		2
DICOTYLEDONES		
Cruciferae	*Brassica rapa*	1
Leguminosae	*Trifolium subterraneum*	1
	Trifolium repens	1
Polygonaceae	*Rumex acetosella*	1
Compositae	*Hypochaeris* sp.	1

bias exists for this species also.

Aquatic animal material appears to be an important part of the diet of Greys and Mallards. Six of the seven ducks examined contained food in this category. Snails - in particular *Potamopyrgus antipodarum* - appeared to be a major constituent of the diet of the ducks examined. The oesophagus of one of the birds was extended to capacity with snails (mostly *Potamopyrgus*). No aquatic vegetation was found in this duck at the time of examination, although remains of this material were found in three of the other ducks.

On the other hand the Canada Geese in the study area are probably almost wholly grazers (during May, if not throughout most of the rest of the year also). Only terrestrial leaf material was present in both birds examined.

In feeding ecology the Paradise Shelduck appears to lie somewhere between the "dabbling species" and the geese.

2) Helminth Fauna

Twenty nine species of helminth parasites were recovered from the birds above. Of these 11 were cestodes, nine were trematodes and nine were nematode species. These included six species of cestode, three species of trematode and four of nematode which were not recovered from *T. variegata*.

a) Mallard and Grey Ducks - Rind (1974) combined data from Mallard and Grey Ducks (which she collectively termed "Wild ducks"). She detected no specificity of parasites for either of these host species. Accordingly, I have also grouped the helminth data of these species from the study area for comparison with those of the Paradise Shelducks. As they were all obtained during May, a comparison of this section can be made directly with the data for Paradise Shelducks given in Section II, Chapter VI.

As for the Paradise Shelducks from the study area it was found that no acanthocephalans were present in the Mallard and Grey Ducks - although Rind (1974) has found members of this group in these ducks obtained from estuarine areas. However, Cestoda, Trematoda, and Nematoda were all represented. Species found infecting the gastrointestinal tracts of the Mallard and Grey Ducks are shown in Table 13 and the incidences and intensities of infections are included. In addition to species from the gastrointestinal tracts, two other trematode species - *Dendritobilharzia pulverulenta* and *Typhlocoelum* sp. were also recorded.

Of the trematode species found infecting the Grey Ducks and Mallard, *U. gippyensis, Catatropis* sp., *E. revolutum, Cotylurus* sp., *D. pulverulenta, P. oxyuris* and *Typhlocoelum* sp. have all been reported from these hosts previously by Rind (1974). The other species found during the study have not been recorded previously from New Zealand Grey Ducks, although *D. flavescens* and *F. fasciolaris* have both been reported from the Australian sub-species, *A. superciliosa rogersi* (Johnston, 1912).

As was seen for the Paradise Shelduck, *C. megalops* has a very high incidence in the dabbling ducks from the study area. However, as in the shelduck, it is rarely present in large numbers. On the other hand, *F. fasciolaris* and *A. furcigera,* which also appear to have high incidence levels in the dabblers, are present in much higher numbers. Of the other cestode species present, only *G. cygni* and *D. flavescens* were present in more than half of the birds. Neither of these species was present in *T. variegata*.

Cestodes are normally typical inhabitants of the lower gastrointestinal tract, and so in this respect, *G. cygni* is an extremly unusual species. It is found only under the koilin lining of the gizzard of its host. Heck (1958) discussed the morphology, taxonomy and incidence of the species in North America.

Five of the 10 cestode species found in the lower alimentary tracts of the Mallard and Grey Ducks during the present study, were also recorded from the Paradise Shelducks. However, only two of these were recovered from shelducks collected at the same time of the year as the Mallard and Grey Ducks (during May). It has already been pointed out that young birds during the spring and summer months tend to harbour parasites not normally present at other times of the year. Thus, it becomes obvious that

Table 13. HELMINTH SPECIES INFECTING THE GASTROINTESTINAL TRACTS OF SEVEN MALLARD AND GREY DUCKS FROM THE STUDY AREA.

	Incidence (no. birds infected)	Intensity (no. per infected bird)	
		Mean	Range
CESTODES			
*Cloacotaenia megalops**	7	9.4	1-20
*Fimbriaria fasciolaris**	6	54.7	8-141
*Aploparaksis furcigera**	6	104.3	7-315
*Anomotaenia ciliata**	2	25.0	9-41
Gastrotaenia cygni	4	18.0	4-45
Diorchis flavescens	5	51.8	2-194
*Sobolevicanthes gracilis**	1	1.0	1
Hymenolepis sp. 1	2	78.5	30-127
Hymenolepis sp. 2	1	2.0	2
Cestode A	1	1.0	1
Cestode B	2	26.0	2-50
TREMATODES			
*Echinostoma revolutum**	4	27.8	1-66
Psilotrema sp.	4	87.0	20-208
*Cotylurus cornutus**	5	12.8	1-51
Catatropis sp.	4	138.3	10-347
*Uniserialis gippyensis**	2	3.5	3-4
Psilochasmus oxyuris	1	9.0	9
NEMATODES			
*Amidostomum acutum**	6	21.5	1-51
*Epomidiostomum uncinatum**	5	15.0	2-50
Echinuria uncinata	3	3.7	2-7
*Capillaria anatis**	4	2.5	1-4
Capillaria contorta	1	7.0	7
Tetrameres sp.*	6	3.7	2-6
Desmodoceridae gen. undet.	1	1.0	1

* Recorded from Paradise Shelducks also

Mallard and Grey Ducks normally possess a cestode fauna of much greater diversity than do Paradise Shelducks. By comparing Table 6 with Tables 13 and 14 it can be seen that intensities of cestode infection are also much higher in the dabblers.

Five species of trematodes were common to both Paradise Shelducks and the dabblers. However, only three of these, *E. revolutum, C. cornutus* and *U. gippyensis* inhabit the gastro-intestinal tracts (see Table 13). Of the other two - *D. pulverulenta* is a blood parasite and *Typhlocoelum* sp. inhabits the respiratory system. *Psilotrema* sp. and a notocotylid *Catatropis* sp. were by far the most numerous trematodes of the Mallard and Grey Ducks. Yet strangely these species were never found in the Paradise Shelduck. Although *Psilochasmus oxyuris* was not found infecting the shelducks this was less surprising as it was not common in the dabblers either.

Two common species from the Paradise Shelduck - *Echinoparyphium recurvatum* and *Notocotylus tadornae* - which could have been expected to be present in the Mallard and Grey Ducks, also, were not found. Both *E. revolutum* and *C. cornutus* which have similar life cycles to *E. recurvatum* were common in these hosts. However, *E. recurvatum* is known to be quite capable of infecting both these host species (S. Rind, pers. comm.). *Notocotylus tadornae* on the other hand, despite being very common in *T. variegata* from a variety of areas, has apparently not been found occurring naturally in the Grey Duck or Mallard. Successful experimental infections with *N. tadornae* in young Pekin-Aylesbury cross ducklings (*Anas platyrhynchos*) during the present study, is the only evidence that this species can parasitise hosts other than the Paradise Shelduck.

It thus appears that while both *T. variegata* and the dabbling ducks are commonly infected by notocotylid trematodes, these are of different species and there is little or no natural interchange between them. This may be due to parasite specificity, interspecific competition or a combination of both factors.

Table 14. COMPARISON OF CESTODE, TREMATODE AND NEMATODE INVASIONS OF THE LOWER GASTRO-INTESTINAL TRACTS OF SEVEN MALLARD AND GREY DUCKS FROM THE STUDY AREA IN MAY.

	Incidence (no. infected)	Intensity (no./infected bird) mean	Intensity (no./infected bird) range	Diversity (no. spp./bird) mean	Diversity (no. spp./bird) range
Cestodes	7	220.3	38-588	4.7	3-10
Trematodes	7	156.0	7-415	2.9	2-4
Nematodes	4	2.5	1-4	1.0	0-1
All helminths	7	377.7	118-995	8.1	5-13

Trematode diversity is apparently relatively low in Mallard and Grey Ducks compared with cestode diversity (Table 14). In May at least, the trematode diversity, while a little higher than in Paradise Shelducks, appears to be comparable. The intensity of infections, however, seems to be somewhat greater in the Mallard and Grey Ducks (compare Tables 6 and 14).

Four species of nematodes were recovered from the Mallard and Grey Ducks which were also found in *T. variegata* (see Table 13). Two of these - *A. acutum* and *E. uncinatum* - the most common species present, were found only in the gizzard, and thus there is no comparable quantitative data from the Paradise Shelduck for these species. Nevertheless, it is known from the incomplete investigation made on the species numbers in the shelducks, that they are much more numerous in the dabbling ducks.

A much wider range of nematode species was found from the oesophagus and proventriculus regions of the dabblers. Species such as *Echinuria uncinata, Capillaria contorta* and the Desmoceridan species - all from these regions - were never found in the shelducks. *Tetrameres* sp. was comparatively common in the *Anas* species, but only one individual was found throughout the entire shelduck sample. *Capillaria anatis* was the only nematode found in the lower alimentary tracts of the Gret Ducks and Mallard. Although three nematode species were present in the lower regions of the tract of shelducks in May, only *C. anatis* was numerous enough to be expected in a sample of only seven birds. Thus, the nematode fauna of the lower tracts of the dabbling species is very similar to that of the shelducks, while that of the upper tract appears considerably more diverse and of greater intensity.

b) Canada Geese - Only two geese were examined - a juvenile bird collected in May 1973 and an adult from May 1974. Both had relatively small burdens and their helminth fauna was very similar in diversity and intensities of the species present. Tables 15 and 16 summarise data on the helminths recovered.

Table 15. HELMINTH SPECIES INFECTING THE GASTRO-INTESTINAL TRACTS OF TWO GEESE FROM THE STUDY AREA.

	Incidence (no. infected)	Intensity (no./infected bird) mean	range
TREMATODES			
*Echinostoma revolutum**	2	6.5	5-8
*Cotylurus cornutus**	1	2.0	2
*Uniserialis gippyensis**	1	6.0	6
*Notocotylus attenuatus**	1	11.0	11
NEMATODES			
Amidostomum anseris	2	7.5	4-11
*Trichostrongylus tenuis**	2	37.5	16-59

* Recorded from Paradise Shelducks also

Trichostrongylus tenuis, which was a rare parasite of the Paradise Shelduck, was relatively common in the caeca of the geese, while *Amidostomum anseris*, a larger species than that found in the gizzards of the Paradise Shelduck (and Greys and Mallard), was also present in both birds. The families Echinostomatidae, Notocotylidae and Strigidae were represented by species also found in the Paradise

Shelduck. Neither goose was infected with cestodes, although trematodes and nematodes were quite well represented. It is uncertain whether this is a chance phenomenon or if it reflects a low rate of cestode infections among the Canada Goose population in the study area. The species feeding habits tend to support the latter idea, but further data would be necessary to provide more conclusive results. Because it is a grazing species it could be expected that nematodes - particularly those with a direct life history - would be present. Trematodes too could be expected to be represented as geese grazing on partially submerged vegetation would be likely to pick up snails or metacercariae on that food. However, one would expect cestodes to be present less frequently, because it is probably primarily by "dabbling" feeding behaviour that their intermediate hosts are ingested.

Table 16. INVASION OF THE LOWER GASTRO-INTESTINAL TRACTS OF TWO CANADA GEESE FROM THE STUDY AREA BY TREMATODES AND NEMATODES.

	Incidence (no. infected)	Intensity (no./infected bird)		Diversity (no. spp./bird)	
		mean	range	mean	range
Trematodes	2	16.0	16	2.5	2-3
Nematodes	2	37.5	16-59	1.0	1
All helminths	2	53.5	32-75	3.5	3-4

3) Conclusions

There seems to be an inverse relationship between the importance of grazing in a waterfowl species' feeding ecology and the size and diversity of its cestode fauna. This may extend to nematode species with an indirect life history. Trematodes do not show this relationship. Undoubtedly the type of intermediate host involved in the life history is important in this respect. Snails are probably often ingested by grazing hosts because they tend to be found on aquatic vegetation, while most crustaceans and oligochaetes are planktonic or benthic and thus less often ingested by grazers. Because trematodes utilize predominantly mollusc intermediate hosts and cestodes and nematodes mainly arthropods or oligochaetes, one could expect a better representation of trematodes in a grazing waterfowl species, than expected for cestodes or nematodes with indirect life histories. On the other hand, a larger proportion of cestodes and nematodes with indirect life histories could be expected in a dabbling waterfowl species.

II. OTHER SHELDUCK SPECIES

The taxonomic relationships of *T. variegata* with the other species of shelduck, and the ecology of members of the group, have been briefly discussed in Chapter III. The parasites of *T. variegata*'s closest relations (the other members of the Casarca group), are very poorly known. It appears that no study of the helminth fauna of *T. cana*, the South African Shelduck, has been made (pers.comm., J.N. Geldenhuys). Up until 1960 the only helminths described from the Australian Shelduck, *T. tadornoides*, were *Echinostoma revolutum*, *Hymenolepis lamellata* and *Syngamus trachealis* (Lapage, 1961). No further work has been published. *Hymenolepis simplex*, *Amidostomum anseris* and *Polymorphus marilis* are the only helminths reported from *T. cristata* (McDonald, 1969).

Much more is known of the helminth fauna of the European member of the Casarca group, *T. ferruginea*. The bulk of the helminth studies on this host have been carried out by workers in the Balkan countries and India. Species recovered from *T. ferruginea* and the other shelduck species (Lapage, 1961 and McDonald, 1969) are listed in Appendix 4). A much wider variety of helminths has been reported from *T. ferruginea* than were recovered from *T. variegata* during the present study. Seventeen species of trematodes, 16 species of cestodes, eight species of nematodes and two acanthocephalans have been reported from *T. ferruginea*. This is probably not surprising considering the wide geographical range over which the European species has been investigated. Of the species reported from *T. ferruginea*, four trematode, four cestode and two nematode species (all of which are geographically cosmopolitan) were also found parasitising *T. variegata.*

Of the other two less closely related species of *Tadorna, T. radjah* is virtually unstudied. Only *Hymenolepis lamellata* has been recorded from this species (McDonald, 1969). Relatively more is known of the parasites of *T. tadorna.* Nineteen species of trematodes have been found infecting *T. tadorna* (Appendix 4), nine of which are known to infect waterfowl in the present study area. However, only five of these are known from the Paradise Shelduck - *E. revolutum, H. conoideum, E. recurvatum, C. cornutus, N. attenuatus,* and possibly *Typholocoelum* sp. Eleven species of cestode have also been reported from *T. tadorna,* but only three of these - *F. fasciolaris, C. megalops* and *S. gracilis* - were found in waterfowl from the present study area. All three infected *T. variegata. Tadorna tadorna* has three recorded nematode species in common with *T. variegata.* As was the case for *T. ferruginea,* two acanthocephalan species are known from *T. tadorna.*

Although there are differences between the ecology of *T. variegata* and the two less closely related shelducks, *T. tadorna* and *T. radjah,* they undoubtedly have more species in common than are known at present. Nevertheless, it is believed that as more is known of shelduck helminths, the greatest similarity of parasite faunae will lie between the members of the Casarca group.

CHAPTER VIII

GENERAL DISCUSSION AND CONCLUSIONS

I. COMPOSITION AND DYNAMICS OF THE HELMINTH FAUNA

Aspects of the ecology of both the host (the Paradise Shelduck) and its parasitic helminth fauna have been examined. How then are these aspects inter-related to produce the composition and dynamics characteristic of the helminth fauna of the Paradise Shelducks?

In Chapter III it was shown that Paradise Shelducks are adapted to a less aquatic life than most other types of waterfowl (with the exception of geese). Although aquatic vegetation forms part of its diet, the Paradise Shelduck is basically a grazing species, feeding for most of the year on pasture plants (particularly grass and clover), or other vegetation in damp places (undoubtedly sometimes partly submerged in shallow water). It rarely "dabbles" or seeks animal material as a normal part of its diet. Because only a small proportion of most Paradise Shelducks' diet is of truly aquatic origin, and very little of this is invertebrate material, large burdens of most helminth species are rare.

In terms of incidence and intensity of infections, the most successful helminths of the Paradise Shelduck are trematodes of the family Notocotylidae. Two factors are probably responsible for their success. Firstly, transmission from final host to intermediate host is well adapted to either still or slow-flowing water, and secondly, transmission to the final host is accomplished by the ingestion of encysted infective larvae on submerged vegetation near the water's surface. Notocotylid transmission is therefore far more closely adapted to the Paradise Shelduck's feeding ecology than is that of any other helminth group found infecting this host. *Notocotylus tadornae* and *Uniserialis gippyensis* were the most numerous notocotylids found in the shelducks. Their intermediate host, *Potamopyrgus antipodarum,* is probably the most abundant and widespread snail in the shelduck's feeding areas.

Another notocotylid species found in the shelducks during the study - *Notocotylus attenuatus* - was less successful in terms of incidence of infection. This may be because *N. attenuatus* can only use lymnaeid snails as intermediate hosts. Snails of this family have a rather localised distribution in the study area, and probably throughout the shelduck habitat in the South Island. *Catatropis* sp. (possibly *verrucosa*), a further notocotylid species, is very common in Grey and Mallard ducks in the study area, and like *N. tadornae* and *U. gippyensis*, it appears to use *P. antipodarum* as an intermediate host. It is therefore surprising that this species was never found in *T. variegata*. The reason for its absence from the helminth fauna of the Paradise Shelduck is unknown. There is undoubtedly a large reservoir of the species in Mallard and Grey Ducks in the study area and so there is a constant source of infection for the intermediate hosts. It is therefore unlikely that there is a lack of opportunity for invasion of shelducks. It is interesting to note that the reverse situation apparently exists for *N. tadornae*. This species was not found in the Mallard or Grey Ducks from the study area. Although there generally seems very little specificity for definitive hosts amongst helminths of waterfowl, *N. tadornae* and *Catatropis* sp. do seem to show a fairly high degree of specificity.

None of the other trematodes found in the Paradise Shelducks reach their host by direct encystment on vegetation. Most - those in the families Echinostomatidae, Strigeidae and Cyclocoelidae - encyst within a molluscan intermediate host and await ingestion by the final host. Three main factors may explain why these species are not as numerous in the Paradise Shelduck as the notocotylids:

1) The host snails of these species, *Gyraulus corinna* and *Lymnaea* spp. are much less numerous than *Potamopyrgus antipodarum* in the study area and probably throughout most of the high-country habitat of the Paradise Shelduck.

2) Much of the water in such habitats is flowing to some extent, and these species are not well adapted to invading snails in such conditions. Still water would normally be

necessary for invasion of intermediate hosts to be most successful. 3) Because snails are normally only eaten incidentally to submerged plant material, transmission to a shelduck host by these species has a much lower potential than that of the notocotylids. Nevertheless, large numbers of them are occasionally present particularly if the host is young or regularly feeds in the same area as a group of Grey or Mallard ducks.

The schistosome trematode *Dendritobilharzia pulverulenta* was the only species found whose cercaria actively penetrate the final host. Although they were not specifically searched for on a regular basis, they were not uncommonly found in the shelducks. However, their numbers are probably limited to some extent by the time which the shelducks spend on still water. Dabbling ducks could be expected to be much more prone to infection.

Cestodes are not as well represented in the Paradise Shelducks as they are in the Mallard and Grey Ducks from the study area. Although most of the cestode species found in the Mallard and Grey Ducks probably occasionally infect Paradise Shelducks as well (particularly very young birds), they are generally present in the shelducks at a much lower incidence and intensity, and the diversity of species per bird is also much lower. The intermediate hosts of the cestodes found are mainly aquatic crustaceans. In general aquatic crustaceans are not ingested intentionally by feeding shelducks, and with the exception of ostracods, do not seem to be as prone as snails to being ingested accidentally with aquatic plant food. Thus the life histories of most cestode species encountered during the study, do not appear to be particularly well suited to transmission to a grazing host such as the Paradise Shelduck.

A second factor could possibly have some influence on the cestode fauna. Because cestodes lack an alimentary canal, in general they must absorb their nutrients directly from the host's intestinal contents. On the other hand, while the absorption of some nutrients can take place via the general body surface of many intestinal trematodes, most probably feed to a larger extent on semi-digested intestinal food contents, together with mucus and mucosal cells derived from the intestine, and released blood (Smyth, 1966). Strigeids, for example, are adapted to browsing on the surface to which they are attached (Smyth, 1966), and *Uniserialis breviserialis* has been shown to feed to a large extent on blood cells (Stunkard, 1967). Cestodes may therefore be more directly affected by the diet of their hosts than are most trematodes and nematodes. Thus, waterfowl species such as the Paradise Shelduck, which feed mainly on vegetative plant material, may simply not provide as favourable an environment for many cestode species, as that provided by dabbling ducks.

Only two cestode species were commonly found in the shelducks. *Cloacotaenia megalops* was the most successful species in terms of incidence, although intensities of infections were never great. Its intermediate host, an ostracod *Herpetocypris pascheri,* is commonly found moving over the sediment amongst vegetation in the slower flowing backwaters of rivers in the study area. The species appears to be one of the commonest and most widespread crustaceans in the riverbed habitat favoured by the shelducks. This, coupled with its apparent proneness to ingestion by the shelducks, may explain the relatively high incidence of *C. megalops* compared with other cestodes. Limited sites in the cloaca of the host possibly restrict the establishment of new infections, and thus may be responsible for the low intensities of infections by this species.

The intermediate host of *Fimbriaria fasciolaris* in the study area is uncertain. However, from an overseas study (Jarecka, 1961), it seems likely that it is normally a copepod species. Copepods probably do not have such a wide distribution as ostracods in the shelduck's usual feeding areas, as they seem more restricted to bodies of still water. Nevertheless, they can become very numerous in such places. Davies (1938) has pointed out that constant water movement tends to retard the population growth of most planktonic crustaceans, and has a profound effect on the rate of ingestion of cestode eggs by such species. Possibly for this reason, and because infection of shelducks depends on whether such a place is regularly included in their feeding area, *F. fasciolaris* occurs in a smaller proportion of the shelducks than does *C. megalops* even although burdens of *F. fasciolaris* are often larger. Three other species of cestodes, *Anomotaenia ciliata, Aploparaksis furcigera* and *Sobolevicanthus gracilis,* were found in the Paradise Shelducks only rarely (although they were apparently much more common in Mallards and Grey Ducks from the same area). It is difficult to say whether the life histories of these species, or their physiological needs in the final host are responsible for their rareness in the shelduck. However, the life cycles of *A. ciliata* and *A. furcigera* do not seem well suited to transmission to shelducks. The intermediate host of *A. ciliata* has been shown to be a planktonic cladoceran while that of *A. furcigera* is an aquatic oligochaete (Jarecka, 1961). Neither of these seems likely to be ingested frequently with aquatic plant food. This may explain their rareness in the shelducks. The life history of *S. gracilis* however, gives no explanation of this species' rareness. A number of copepod and ostracod intermediate hosts have been reported for it (MacDonald, 1969), several of which have also been reported to be utilised by *F. fasciolaris*. *Sobolevicanthus gracilis* therefore could have been expected to have been as common in the shelduck as *F. fasciolaris,* yet only a single specimen was found throughout the study.

Like some of the other helminth species of the Paradise Shelduck, the three cestode species above occurred so rarely that their presence may be considered "accidental". In general such species were restricted to young birds and it is doubtful if most could maintain their presence in Paradise Shelducks without a constant reinfection of intermediate hosts by other members of the species established in more suitable final hosts (in most cases Mallard or Grey Ducks).

Some nematode species such as *Trichostrongylus tenuis, Tetrameres* sp. and *Syngamus?* sp. appear to fall into this category. *Trichostrongylus tenuis* may have been acquired from geese in which the species seems common, while *Tetrameres* sp. is normally a parasite of Mallards and Grey Ducks in the study area. Despite their rarity, both species appear to be reasonably well suited for transmission to shelducks. *Tetrameres* sp. requires an intermediate host. Yet, presuming this species has a life cycle similar to *T. fissispina,* a very wide range of hosts can be utilised - including insect larvae, aquatic crustaceans, platyhelminths, and oligochaetes. *Trichostrongylus tenuis* on the other hand, has a direct life history very similar to that of *Capillaria anatis*. Yet while *C. anatis* is the commonest nematode of the shelducks, *T. tenuis* is rare.

Like *C. anatis,* the two gizzard nematodes, *Amidostomum acutum* and *Epomidiostomum uncinatum* have direct life cycles, and both were present in the shelduck quite frequently.

Porrocaecum crassum was present infrequently, but its presence cannot be regarded as "accidental". Either an oligochaete or insect larva is required as an intermediate host for transmission of this species. As a general rule however, nematodes with indirect life histories were poorly represented in the shelducks (compared with their diversity and intensity in Mallard and Grey Ducks).

The nematodes of waterfowl in the study area which require intermediate hosts possess life histories which closely resemble those of cestodes. It appears that both nematodes with indirect life histories and cestodes are poorly represented in Paradise Shelducks for similar reasons. As both these groups are well represented in the dabbling ducks from the same area, it seems probable that the unsuitability of their life histories for transmission to shelducks is a major cause of their lack of success in the shelducks.

Fluctuations in seasonal patterns of helminth infections appear to be present in the case of some species, but they are not great. Seasonal diet changes of the shelducks may be in part responsible for dampening fluctuations in helminth invasions. The fruiting season of most plants accessible to shelducks, coincides with the increase in numbers of most aquatic invertebrates.

It was shown in Chapter III that "berries" form an important part of the shelduck's diet during the spring and summer (possibly to the exclusion of a proportion of aquatic foods). Thus, as "berries" probably form an even more sterile diet from the point of view of helminths than pasture plants, the invasions by helminths did not increase dramatically in summer despite an increase in numbers of intermediate hosts. The highest infection rate by many helminth species (apart from those in young shelducks during the breeding season), appeared to be during autumn, i.e. when "berries" became unavailable but aquatic invertebrates were still numerous and easily accessible to the shelducks. It is also probably during early autumn that the highest proportion of intermediate hosts of most species are infected. Diet and the abundance of intermediate hosts are probably not the only factors affecting helminth abundance on a seasonal basis. Infections by one trematode - *U. gippyensis* - decreased through the winter more dramatically than most, because its main habitat in the definitive host - the bursa of Fabricius of juvenile birds - slowly degenerates during this time.

Helminths in general have a higher incidence and intensity in juvenile shelducks than in adults, and the average number of species per juvenile bird is also higher. This difference in helminth burden is particularly pronounced in juveniles in their first three months - up until the time they fly - although it is still present to a smaller extent in six month old birds. Two factors may be involved in bringing about the differences in helminth burdens seen between adults and juveniles. Once able to fly young birds can leave the rather restricted areas in which they were raised, and thus feed in other areas which are possibly less contaminated with helminths. A build up in immunity to re-infection during the first few months probably also influences the size and diversity of the helminth fauna present.

Because the presence of man has caused a change in the distribution and numbers of the Paradise Shelduck, his actions have probably also had a considerable influence on the composition of the helminth fauna of the shelducks.

The large reduction in the numbers of Paradise

Shelducks over the last two decades (Williams, 1971), the drainage of areas of wetland, and the great increase in areas of exotic pasture throughout a great deal of the Paradise Shelduck's range, may have brought about a reduction in numbers of indigenous helminths infecting this species. The reductions in size of local concentrations of shelducks must have brought about a reduction in the infection rate of intermediate host populations (though the territorial behaviour of the Paradise Shelduck may have damped this effect), while the drainage of wetland has probably reduced the populations of some types of intermediate hosts. The reduction of native forest and increase in areas of pasture has meant that the shelducks are less confined to riverbed areas and has undoubtedly meant a change to a much more sterile diet (from the point of view of most helminth infections).

At the same time there may have been an increase in the diversity of parasites infecting New Zealand's waterfowl species, due to the introduction of both exotic snails, and domestic and wild waterfowl.

However, self-introduction of waterfowl species particularly from Australia, over the past has probably been the means by which the majority of helminths have arrived here. In recent years several Australian species including the Australian Shelduck *T. tadornoides* (Oliver, 1955), have been recorded here as stragglers, and some such as the Grey Teal *Anas gibberifrons* are currently breeding here (O.S.N.Z., 1970).

II. PATHOLOGY OF HELMINTHS

A number of the helminth species found in waterfowl from the study area during the present study, have been considered by previous authors to have been responsible for the death of their hosts. Keymer *et al.* (1962) listed the helminths of wild and game birds in Great Britain which have been implicated, and among these are *Echinoparyphium recurvatum*, *Hymenolepis (Sobolevicanthus) gracilis*, *Fimbriaria fasciolaris*, *Amidostomum anseris* and *Trichostrongylus tenuis* - all of which are present in the study area. They found 338 of the birds which they examined to be infected with helminths, and attributed the deaths of 64 of these to their helminth burdens. Soulsby (1968) considered a number of helminth species to be of veterinary importance. While he stated that the Notocotylidae were rarely associated with pathologic effects, he listed many other helminths which have been. He discussed the pathogenic effects and treatments of several species found during the present study, among which are *Hypoderaeum conoideum, Echinostoma revolutum, Echinoparyphium recurvatum,* the members of the Strigeidae, *Typhlocoelum* sp. *Capillaria contorta, Tetrameres* sp., *Echinuria uncinatum, Trichostrongylus tenuis* and *Amidostomum anseris.* With reference to *A. anseris*, he says that this species is very pathogenic to young geese, while the adult birds may act as carriers of infection without showing clinical signs.

The problem of assessing pathology of parasites to their wild host species is a particularly difficult one in a survey such as this. On the surface a simple correlation of the host's physical condition with its parasite load would seem to provide information on pathology. The physical condition can be estimated in various ways, e.g. Kidney fat index (Riney, 1955), Emaciation index (Cornwall and Cowan, 1963). However, any such index is stratified by age, sex, individual variation and geographical location of the host and by the time of the year.

Assessing the intensity of overall helminth burdens is often even more difficult as mixed infections generally complicate the issue. Obviously the effect of 100 small helminths will not be the same as 100 much larger species, and that of 100 cestodes will not be the same as 100 tissue feeding species. To get comparative values for the intensities of helminth burdens of different ducks infected with different species is not possible at this stage. Nevertheless, it is possible to say that of all birds collected in May 1971, 1972 and 1973, none appeared to be in poor condition because of the size of its helminth load. However, compared with parasite loads of young birds during summer, none was very heavily infected with helminths (see Chapter VI).

Young birds, particularly while still flightless, tend to carry much heavier helminth burdens than older birds, and it is probably at this early age - before the acquisition of immunity - that large helminth burdens have their most harmful effect. Mortality amongst young waterfowl of most species is relatively high, and shelducks are no exception. It would be interesting (and valuable) to know what percentage of the mortality of young shelducks (and other waterfowl species) is caused either directly or indirectly by helminths. Even if their death is not always caused directly by the helminths present, it seems quite likely that many young shelducks succumb for various reasons as a result of being weakened by large helminth infestations. It is very difficult to check on this however, as dead or even weak shelducklings are very rarely found in the open. Once weak and separated from their brood-mates they probably tend to make for cover. Those that die in the open are quickly devoured by predators. It is conceivable that in certain localities - particularly in confined swamps or ponds which are used regularly by other waterfowl - young broods of ducklings suffer considerable mortality, due either directly or indirectly to helminth parasite invasions.

CHAPTER IX

SUMMARY

1) This work investigates the range and dynamics of the helminth parasites which infect the Paradise Shelduck *Tadorna variegata* in its natural habitat, and attempts to relate these as far as possible to aspects of the ecology of the host and the life histories of the parasite species involved.

2) The Paradise Shelducks were sexed initially from the sexually dimorphic colours, but determinations were always checked on dissection. They were aged according to the presence or absence of the bursa of Fabricius - those possessing bursae were considered to be not more than one year old.

3) The diet of the shelducks consisted in the main of terrestrial vegetative material (particularly leaves of grasses, clovers, rushes, sorrell and dandelion), but also included some seeds of these species and a small amount of both aquatic plant (particularly filamentous algae) and animal material. The animal material consisted mainly of aquatic larval stages of insects (particularly caddis flies) and snails, and most was almost certainly ingested incidentally with plant material. "Berries" of *Muehlenbeckia axilaris, Gunnera dentata,* and *Cyathodes fraseri* were favoured foods in season, as were flower buds of *Hypochaeris* sp.

4) The helminth species recovered were: Cestodes: *Aploparaksis furcigera, Cloacotaenia megalops, Sobolevicanthus gracilis, Fimbriaria fasciolaris, Anomotaenia ciliata*; Trematodes: *Cotylurus cornutus, Echinostoma revolutum, Echinoparyphium recurvatum, Echinostoma* sp., *Hypoderaeum conoideum, Notocotylus attenuatus, Notocotylus tadornae* n.sp., *Uniserialis gippyensis, Typhlocoelum* sp. (possibly *cucumerinum*), *Dendritobilharzia pulverulenta*; Nematodes: *Capillaria anatis, Amidostomum acutum, Epomidiostomum uncinatum, Trichostrongylus tenuis, Tetrameres* sp., *Porrocaecum crassum* and Syngamidae gen. undet.

5) Each helminth species was normally restricted to

a certain region of the host's body. *Tetrameres* sp. occupied the proventriculus, while *A. acutum* and *E. uncinatum* were never found outside the gizzard. The usual location of *F. fasciolaris, S. gracilis, A. ciliata, C. cornutus, E. recurvatum* and *P. crassum* was the anterior half of the small intestine. Other species found in this region such as *H. conoideum* and *E. revolutum* tended to be less restricted in their location, with *H. conoideum* apparently occupying the whole length of the small intestine, and *E. revolutum* occupying all regions of the lower alimentary tract with similar frequency. *Notocotylus tadornae, N. attenuatus, C. anatis* and *T. tenuis* were all normally located in the host's caeca, while *Echinostoma* sp. favoured the large intestine and *C. megalops* the cloaca. *Uniserialis gippyensis* was occasionally found in the cloaca but was normally within the bursa of Fabricius of young birds. Of the two trematode species found which were not intestinal parasites, *D. pulverulenta* occupied the blood vessels of the liver region, and *Typhlocoelum* sp. was apparently within the host's air sacs. The site the undetermined syngamid species occupied is unknown.

6) A new species of notocotylid trematode *Notocotylus tadornae* from the Paradise Shelduck is described and its life history examined; the intermediate host is an hydrobiid snail *Potamopyrgus antipodarum.* The life history of *Uniserialis gippyensis* is described for the first time and it is shown that its intermediate host is also *Potamopyrgus antipodarum,* while the intermediate host of *Cloacotaenia megalops* in New Zealand was found to be an ostracod *Herpetocypris pascheri.*

7) The life histories of the other helminths found in the Paradise Shelduck are reviewed. The intermediate hosts of most of the remaining trematodes are lymnaeid or planorbid snails, and those of the cestodes probably include a variety of aquatic invertebrate species. Life cycles of the nematodes of the Paradise Shelduck are mostly direct. Those which are not, utilise aquatic invertebrates or possibly, in the case of *Porrocaecum crassum,* an earthworm.

8) Of a total of 181 shelducks collected during May

1971, 1972 and 1973, 97.8% were infected with intestinal helminths. The mean number of helminths per infected bird was 46.4, although the variety of helminths simultaneously infecting each bird was not great - an average of only 3.17 species per bird. Trematodes as a group were the most frequently encountered helminths, followed by cestodes and nematodes respectively.

9) Juvenile shelducks, particularly while still flightless, were found to be much more heavily infected with helminths than were adults. However, by the time the juveniles were aged six months (in May), their helminth burdens resembled those of adults much more closely, although some differences were still present. In the case of two helminth species - *Cloacotaenia megalops* and *Cotylurus cornutus* - a significantly greater proportion of adult shelducks was infected, while *Uniserialis gippyensis, Notocotylus tadornae* and *Echinostoma revolutum* infected a significantly greater proportion of juveniles.

10) With the exception of one species, helminth infections did not differ significantly between male and female shelducks. The intensity of infections by *Uniserialis gippyensis* was much greater in males than in females.

11) Seasonal changes in helminth infection of the Paradise Shelduck are not marked. However, it appears that the period of greatest infection in terms of the overall population, is during the autumn before the colder weather reduces the intermediate host populations. At this time "berries" are no longer an important part of the shelduck's diet and the infection rates of the intermediate host populations are probably at a peak.

The peak infection rate of juveniles alone, however, occurs before they have fledged during the summer.

12) Seven dabbling ducks (Mallard and Grey) from the study area, were found to have fed on aquatic material more extensively than the shelducks, and aquatic animal material appeared to be a major part of their diet. Their helminth fauna was much more diverse than that of the shelducks (particularly in the case of cestodes and those

nematodes whose life histories were indirect), and in general they were much more heavily infected.

In all 29 species of helminth parasites were recovered from the seven Mallard and Grey Ducks, and of these twelve were not found in any of the 281 Paradise Shelducks.

13) Two Canada Geese from the study area were also examined. The food they contained consisted entirely of terrestrial vegetative material. Neither was infected with cestodes although trematodes and nematodes were quite well represented.

14) A comparison is made between the helminth fauna of the Paradise Shelduck and those known from other shelduck species around the world. The parasite faunae of the shelducks most closely related to the Paradise Shelduck are very poorly known, and no quantitative survey of the helminths of these species has been attempted. It is likely that similarities will become more apparent as our knowledge of these other shelducks increases.

15) It is suggested that the presence of man in New Zealand may have reduced the degree of helminth infection amongst Paradise Shelducks, by reducing and dispersing the shelduck population and by drainage of certain types of wetland which support the most dense populations of intermediate hosts. However, man has probably also introduced a number of different types of helminths by introducing domestic and wild waterfowl and exotic snail species.

16) Results of the study indicate that adult birds rarely carry large burdens of helminth parasites, and hence probably suffer very little mortality due to helminth infections. However, young shelducks particularly while still flightless, were found to carry much heavier helminth burdens than older birds, and it is probably at this early age that large helminth burdens have their most harmful effects. It is possible that helminths are responsible, either directly or indirectly, for the deaths of many young shelducks before they have fledged.

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APPENDIX 1

DATE AND LOCATION OF COLLECTION OF SAMPLES

Year	Location	Date	Number in Sample
1971	Lewis Pass	May 1-2	45
	Lake Ellesmere	May 9	1
	Selwyn River	May 23	6
	Lewis Pass	May 30	25
1972	Lewis Pass	May 6-7	60
			3 Grey Ducks 1 Mallard
	Lake Coleridge	May 6	13
	Selwyn River	May 21	10
	Lewis Pass	May 27	10
	Porter's Pass	June 5	1
	Lewis Pass	June 24-25	10
	"	July 29	10
	"	August 26	3
	"	August 29	7
	"	September 23	10
	"	October 28	10
	"	November 25	10
	"	December 28	10
1973	Lewis Pass	January 27	10
	"	February 24	10
	"	March 31	10
	"	May 5	10
			1 Grey Duck 1 Canada Goose
1974	Lewis Pass	May 4	2 Grey Ducks 1 Canada Goose

<u>NB</u> Figures in right hand column refer to Paradise Shelducks unless otherwise stated.

APPENDIX 2

PHYSICAL CONDITION OF SHELDUCKS COLLECTED BETWEEN JULY 1972 AND MAY 1973

Number	Age Class	Sex	Subab. fat wt (gm)	Body wt. (gm)	Index
JULY					
105	A	F	5.9	1192	0.50
106	J	F	5.1	1120	0.46
107	J	F	4.2	1102	0.38
108	A	F	1.6	1152	0.14
109	A	F	5.8	1201	0.48
110	A	M	2.9	1474	0.20
111	A	M	4.1	1557	0.26
112	A	M	4.3	1542	0.28
113	J	M	20.7	1472	1.41
114	A	M	4.3	1541	0.28
AUGUST					
115	J	M	9.6	1378	0.70
116	J	F	8.5	1104	0.77
117	A	F	2.7	1168	0.23
118	A	M	7.5	1564	0.48
119	A	M	3.7	1421	0.26
120	A	M	3.1	1601	0.19
121	A	M	2.8	1418	0.20
122	A	F	5.6	1186	0.47
123	A	F	23.8	1285	1.85
124	A	F	17.4	1025	1.70
SEPTEMBER					
125	J	F	5.6	1005	0.56
126	J	F	3.5	970	0.36
127	A	F	4.6	1013	0.45
128	J	F	3.0	1014	0.30
129	J	F	4.0	965	0.41
130	A	M	4.0	1545	0.26
131	J	M	10.0	1263	0.79
132	J	M	16.1	1343	1.20
133	A	M	2.0	1377	0.15
134	A	M	21.8	1437	1.52
OCTOBER					
135	J	F	1.2	852	0.14
136	A	F	1.3	1007	0.13
137	J	F	1.1	873	0.13
138	J	F	2.6	980	0.27
139	A	F	1.5	912	0.16
140	J	M	4.5	1363	0.33
141	A	M	1.6	1304	0.12
142	A	M	2.7	1342	0.20
143	A	M	6.9	1308	0.53
144	A	M	4.2	1190	0.35

APPENDIX 2 (continued)

Number	Age Class	Sex	Subab. fat wt (gm)	Body wt. (gm)	Index
NOVEMBER					
145	A	F	2.9	955	0.30
146	A	F	1.6	1090	0.15
147	J	F	3.6	1009	0.36
148	A	F	2.4	995	0.24
149	J	M	0.0	367	0.00
150	J	M	0.0	369	0.00
151	A	M	3.5	1433	0.24
152	A	M	2.9	1422	0.20
153	A	M	4.0	1521	0.26
154	A	M	1.7	1393	0.12
DECEMBER					
155	J	M	1.0	1044	0.11
156	J	M	4.2	1019	0.41
157	A	M	4.9	1388	0.35
158	A	F	2.6	1118	0.23
160	A	F	3.4	1141	0.30
161	A	F	12.5	1201	1.04
162	A	F	5.5	1140	0.48
163	A	F	1.0	1001	0.10
164	A	F	1.7	1139	0.15
JANUARY					
165	J	F	3.3	882	0.37
166	A	F	13.3	1211	1.10
167	A	F	27.8	1187	2.34
168	A	F	40.4	1509	2.68
169	A	F	3.1	942	0.33
170	A	M	1.4	1434	0.10
171	A	M	5.2	1578	0.33
172	A	M	40.8	1774	2.30
173	A	M	1.9	1370	0.14
174	A	M	2.4	1342	0.18
FEBRUARY					
175	A	M	1.8	1174	0.15
176	A	M	3.6	1350	0.27
177	J	M	7.5	1292	0.58
178	A	M	1.6	1260	0.13
179	A	M	2.5	1430	0.17
180	A	F	1.5	1027	0.15
181	A	F	1.6	1060	0.15
182	A	F	2.6	994	0.26
183	A	F	3.0	1192	0.25
184	A	F	1.3	1026	0.13

APPENDIX 2 (continued)

Number	Age Class	Sex	Subab. fat wt (gm)	Body wt. (gm)	Index
MARCH					
185	A	F	3.7	1039	0.36
186	A	F	2.4	1259	0.19
187	A	F	14.2	1186	1.20
188	A	F	3.0	1024	0.29
189	A	F	4.9	1078	0.45
190	A	M	3.2	1290	0.25
191	A	M	5.8	1506	0.39
192	A	M	5.2	1589	0.33
193	A	M	9.8	1472	0.67
194	A	M	11.9	1470	0.81
MAY					
195	A	F	7.7	1139	0.68
196	A	F	9.9	1186	0.83
197	A	F	19.7	1381	1.43
198	A	F	5.5	1243	0.44
199	J	F	37.2	1248	2.98
200	A	M	4.8	1560	0.31
201	A	M	3.9	1511	0.26
202	J	M	36.3	1543	2.35
203	A	M	2.8	1349	0.21
204	J	M	25.3	1380	1.83

A = adults; J = juvenile; F = female; M = male.

APPENDIX 3

HELMINTHS FROM PARADISE SHELDUCKS

KEY: A = Adult; J = Juvenile; F = Female; M = Male.

* Species for which data are incomplete because their normal habitats were not systematically searched.

	C. megalops	*F. fasciolaris*	*A. furcigera*	*S. gracilis*	*A. ciliata*	*U. gippyensis*	*N. tadornae*	*N. attenuatus*	*E. recurvatum*	*E. revolutum*	*Echinostoma* sp.	*H. conoideum*	*C. cornutus*	*D. pulverulenta**	*Typhlocoelum* sp.*	*C. anatis*	*P. crassum*	*A. acutum**	*E. uncinatum**	*T. tenuis*	*Tetrameres* sp.	Syngamid*
MAY 1971																						
1 JF		1					51															
2 JF	1	3				2	29															
3 JF						12							1									
4 JF		2				2	4									4						
5 AF													2									
6 AM	3						7						7									
7 AM																						
8 JF						10			1													
9 JF	8					3	2		1													
10 JF		12				3	156						1			3						
11 JF	6	1				2																
12 JM						8																
13 JM	1	1				3	3															
14 JF						4	6															
15 JM	3	15				8	8		3													
16 JF																						
17 JF		1				2	109			2			1									
18 JM							14															
19 AM	4	6																				
20 JM	9	28				14	11									6						
21 JF	16	4																				
22 JM						5																
23 JM	1	4					2															
24 JF	7	1				3																
25 AF							171		4	1						4	1					
26 AF	2																					
27 JF		1				1	9															
28 JM	1	1				5																
29 AF	4						15									2						
30 AM	3						16															
31 JF		13				7	2															
32 JM	1	6					9															
33 JF	5					1	1									1						
34 JM	3					7	68															
35 JF	1					2	2			1						2						
36 JF							3															
37 JF						2																
38 JM	2	52				21	85			1						1						
39 JM	1	1				6	80									2						
40 JM	1	6				21	47			2						6						
41 JF		1				7																
42 JM						5																
43 JM	3	6				3	52															
44 AF	2	3					10						4									
45 AF		1					262			1						3						
46 JF		2				20	16			2												
47 JM	7					8	78			1												
48 AM	13	1							3													
49 AM	12	10					233									2						
50 AF	3						16						3			1						
51 AF	4						6									1						
52 AF	2						1						1									
53 JM		2				17																
54 AM	5	18					17															
55 JM						5							3									
56 AM	1																					
57 AM							62		2							3						
58 AM							24															
59 JM						6							3									
60 JM						11																
61 AM																						
62 JF										2												
63 JM		4				4	7									1						
64 JF	1					3							3									
65 JM	1					5	73									1						

APPENDIX 3 (continued)

	C. megalops	F. fasciolaris	A. furcigera	S. gracilis	A. ciliata	U. gippyensis	N. tadornae	N. attenuatus	E. recurvatum	E. revolutum	Echinostoma sp.	H. conoideum	C. cornutus	D. pulverulenta*	Typhlocoelum sp.*	C. anatis	P. crassum	A. acutum*	E. uncinatum*	T. tenuis	Tetrameres sp.	Syngamid*
66 AM	2						1															
67 JM	2					5																
68 JF	10					2																
69 AM																						
70 AF	5						9															
71 JF						8	3															
72 AM	5																					
73 JM						3	2															
74 JM	5						1		2													
75 JF	8					2																
76 JM	3																					
77 AF	1																					
MAY 1972																						
1 AF							19						1									
2 AF	2	1																				
3 JF	4	12				1	45			4			1			8						
4 JF		2					4											1				
5 AF							63									1						
6 JF	7	3				1	71									15						
7 JF							11															
8 JF	1	2				1										2						
9 JF						3	7						1			1						
10 JF	10	1				2	1									1						
11 JF		1				3	4			1						9		1				
12 AF	1						2						1									
13 AF	5	1				1	128									8						
14 JF						2	11									15						
15 JF	4					1	54															
16 AF	1													2								
17 JF		3				4	1									6				1		
18 JF	6	2				1	27						1			6	1					
19 AF	3	6					127									1						
20 JF	2					2	26		6							13	3	2				
21 JF	14	2				2	58		1	1			1			5				1		
22 JF		1					289		20		3											
23 JF		1					4									6						
24 AF							18									3						
25 AF	2	24					4		24				3			8						
26 JF	5	2				2	7			1			1			2		2				
27 JF						3				7												
28 AF	1	2					26						1									
29 JF		1				14	193									8						
30 JF						1	2															
31 JM		1					31		1							7	1					
32 JM		2					72									2		1				
33 AM						1		160	29				1			14	1					
34 JM		3				3	142									35						
35 JM		1				3	10			1						14		1				
36 JM		1				3	444									25						
37 AM	2						55						1					2				1
38 JM	1					5				1												
39 JM							8									4						
40 JM	7					3	4									7						
41 JM	2	1				6	120									2				4		
42 JM						2	57						1			15		2				
43 JM	1					5			10							2						
44 JM							56									3						
45 AM	1						15															
46 AM	6						205		178				4			5		4				
47 JM		1				34	40						3			1	1					
48 JM		7				2	17						6			15	1					
49 JM	15	10				3	21						1			19						
50 JM						3												1				
51 JM						1	56															
52 JM	2					3	26									11	3	1				
53 JM	1					4	17		2													
54 JM	5					3	38									1						
55 JM	1					4	58															
56 JM						7	48			1												
57 AM	4	1					104									2		2				

APPENDIX 3 (continued)

	C. megalops	*F. fasciolaris*	*A. furcigera*	*S. gracilis*	*A. ciliata*	*U. gippyensis*	*N. tadornae*	*N. attenuatus*	*E. recurvatum*	*E. revolutum*	*Echinostoma* sp.	*H. conoideum*	*C. cornutus*	*D. pulverulenta**	*Typhlocoelum* sp.*	*C. anatis*	*P. crassum*	*A. acutum**	*E. uncinatum**	*T. tenuis*	*Tetrameres* sp.	Syngamid*
58 AM	3															1						
59 JM							58									8						
60 JM	5	3																				
61 AF	1	2					128						4			1						
62 AF	1	1											1									
63 AF	6												2			1						
64 JF	1					3	4															
65 AM	8																					
66 JM		2				4	55						2			1						
67 JF		10					64									1						
68 AF	5	1					21						1									
69 AM	2	2							15													
70 AM	2	1					32						2					1				
71 AM	4						16									7						
72 AF	2						65															
73 AF							5															
74 AM	3	3																				
75 JM	5	1				4	31		1				1			1		1				
76 AM	2	2							1				1	1		1						
77 AM	12																					
78 AM							19															
79 AF	2	1							1				1					2				
80 AF	6	1												1								
81 AF	3																					
82 AF		1							5				1	1				3				
83 AF	6																	1				
84 AF	4	1					31									15		1				
85 JF	1						39									5		2				
86 JF	1					1	3															
87 AF	1						407									8						
88 JF	6					2	70									11						
89 AM	2						1		3							1		3				
90 JM	3					4	1									1						
91 AM	4						2		1							4						
92 JM						7	5									3						
93 JM	7					6	18											1				
94 AF	4	14					1															
JUNE 1972																						
95 JM		1				4	117									1						
96 JM						1	279						2			17						
97 AM	6	2					5		1													
98 AM	2	8					547									1						
99 AM	1	1					1297									3						
100 AF		4					572						3			2						
101 AF	1						19									1						
102 JF	1	2				2	9									2						
103 JF	1					4	479									7						
104 AF							174		46													
JULY 1972																						
105 AF	2																					
106 JF	5	5				4	45									2						
107 JF						1	30									6						
108 AF	1	3														6	1					
109 AF	3						17															
110 AM	8						29		4													
111 AM	1						112															
112 AM	12												5			2						
113 JM						2	116									10						
114 AM	4	9					24															
AUGUST 1972																						
115 JM	3	1				1	5									2						
116 JF						1							2									
117 AF		1					1		4				1	1								
118 AM	9						21									2						
119 AM	1	17				2	446		4				2					9				

APPENDIX 3 (continued)

	C. megalops	*F. fasciolaris*	*A. furcigera*	*S. gracilis*	*A. ciliata*	*D. gippyensis*	*N. tadornae*	*N. attenuatus*	*E. recurvatum*	*E. revolutum*	*Echinostoma* sp.	*H. conoideum*	*C. cornutus*	*D. pulverulenta**	*Typhlocoelum* sp.*	*C. anatis*	*P. crassum*	*A. acutum**	*E. uncinatum**	*T. tenuis*	*Tetrameres* sp.	Syngamid*
120 AM	5								2							4		1				
121 AM	6	2					4		10				3			1						
122 AF																						
123 AF							15			1						1						
124 AF	1												1									
SEPTEMBER 1972																						
125 JF	2	2				2																
126 JF	3	1				3	2									3						
127 AF	2						9									5						
128 JF	7																					
129 JF																1						
130 AM							45									1						
131 JM													3									
132 JM	1				1		1															
133 AM	5						41						4			1						
134 AM																1						
OCTOBER 1972																						
135 JF		1				1	6									2						
136 AF	1	1					48						7			3		1				
137 JF	1						70															
138 JF	2	2					117															
139 AF							4									2		2				
140 JM	6				2																	
141 AM																						
142 AM	4	1					1															
143 JM	1	1					2															
144 AM							23															
NOVEMBER 1972																						
145 AF	4												2					1				
146 AF	1				1								1			2		1	4			
147 JF		1											5			2						
148 AF	2						75											5			1	
149 JM	6	9	8	1		1	152											1				
150 JM		4	8			7	65											2				
151 AM																		1				
152 AM	7						95															
153 AM	6								6													
154 AM	3	2					8									3		2				
DECEMBER 1972																						
155 JM		76			9		5		259			58	1		1	121	12	8				
156 JM		9				131	85		1							1	4					
157 AM	4								19									2				
158 AM																						
159 AF									1									5	1			
160 AF	2																1		8			
161 AF	1															3		1	13			
162 AF	1	1						5	60							6						
163 AF		2						32	85							1	4		3			
164 AF									3							3		1	14			
JANUARY 1973																						
165 JF	1	1						9	139		1					9	3	3		1		
166 AF																2		3				
167 AF		2																				
168 AF									4													
169 AF						256																
170 AM	3					1										1						

APPENDIX 3 (continued)

	C. megalops	*P. fasciolaris*	*A. furcigera*	*S. gracilis*	*A. ciliata*	*U. yippyensis*	*N. tadornae*	*N. attenuatus*	*E. recurvatum*	*E. revolutum*	*Echinostoma* sp.	*H. conoideum*	*C. cornutus*	*D. pulverulenta**	*Typhlocoelum* sp*	*C. anatis*	*P. crassum*	*A. acutum*	*E. uncinatum**	*T. tenuis*	*Tetrameres* sp.	Syngamid*
171 AM	10																					
172 AM	8													2				1				
173 AM	4						164									4						
174 AM	5						2160									10						
FEBRUARY 1973																						
175 AM	8															4						
176 AM		8																				
177 JM		3				26	13															
178 AM	2	3							7							2						
179 AM	3								6													
180 AF		3					31									1						
181 AF																						
182 AF	2																					
183 AF	1													1								
184 AF	1						113									1						
MARCH 1973																						
185 AF	6													1								
186 AF	2	2						11					2	1								
187 AF	4						1															
188 AF	2	9					376															
189 AF	4	6					446						1									
190 AM		65					60		29					1		3						
191 AM	8						9		3													
192 AM	1						60	3						1		1						
193 AM							4							2		1						
194 AM	6	3					8						2			5						
MAY 1973																						
195 AF	4												2			1						
196 AF	5																					
197 AF	1	3							2				4			3						
198 AF	1						71															
199 JF	9					5	46															
200 AM	3						63		4							2						
201 AM	5						28									5		2				
202 JM						2	7			3						2		2				
203 AM	4																					
204 JM	2					8	1									2						

APPENDIX 4

FROM McDONALD (1969) and LAPAGE (1961)

T. variegata		-
T. cana		-
T. tadornoides		*Echinostoma revolutum**
		Hymenolepis lamellata
		Syngamous trachea
T. cristata		*Amidostomum anseris*
		Hymenolepis simplex
		Polymorphus marilis
T. radjah		*Hymenolepis lamellata*
		*Hymenolepis gracilis**
T. ferruginea	Trematodes	*Apatemon gracilis*
		*Cotylurus cornutus**
		Plagiorchis maculosus
		P. ferrugineum
		P. cirratus
		Petasiger longicirratus
		*E. revolutum**
		*E. recurvatum**
		Echinostoma paraulum
		Prosthogonimus cuneatus
		P. anatinus
		Orchipedum tracheicola
		Typhlocoelum sisowi
		Psilochasmus indicus
		P. oxyurus
		*Notocotylus attenuatus**
		Paramonostomum casarcum
	Cestodes	*Anomotaenia ciliata**
		*Aploparaksis furcigera**
		Diorchis acuminata
		D. inflata
		D. nyrocae
		D. ransomi
		D. spinata
		Bisaccanthes bisaccata
		*Cloacotaenia megalops**
		Dicranotaenia coronula
		Retinometra longicirrosa
		*Sobolevicanthus gracilis**
		S. octacantha
		Echinocotyle rosseteri
		Orepanidotaenia signachiana
		Retinometra skrjabini

APPENDIX 4 (continued)

	Nematodes	*Cyathostoma bronchialis* *Amidostomum acutum** *A. anseris* *Porrocaecum crassum** *Tetrameres fissispina* *Echinuria borealis* *E. uncinata* *Streptocara crassicauda*
	Acanthocephalans	*Polymorphus magnus* *P. marilis*
T. tadorna	Trematodes	*Cotylurus erraticus* *C. cornutus** *Hypoderaeum conoideum* *Echinostoma revolutum** *Echinoparyphium recurvatum* *Himasthla elongata* *Psilochasmus oxyurus* *Gymnophallus choledocus* *Catatropis cygni* *C. verrucosa* *Notocotylus attenuatus** *Paramonostomum alveatum* *P. bucephala* *Typhlocoelum cucumerinum* *T. sisowi* *Levinseriella brachysoma* *L. bacephala* *Maritrema subdolum* *Cryptocotyle concavum*
	Cestodes	*Fimbriaria fasciolaris** *Dicranotaenia coronula* *Cloacotaenia megalops** *Drepanidotaenia lanceolata* *Microsomacanthus spiralicirrata* *Lateriporus destitutus* *Parictotaenia borealis* *Sobolevicanthus gracilis** *Diorchis nyrocae* *Hymenolepis simplex* *Dicranotaenia coronula*
	Nematodes	*Echinuria uncinata* *E. hypognatha* *Amidostomum acutum** *A. anseris* *Capillaria anatis** *C. contorta* *Cyathostoma tadornae* *Epomidiostomum crami* *E. uncinatum** *Hystrichis tricolor* *Tetrameres fissispina* *Heterakis dispar* *H. gallinarum* *Streptocara crassicauda*

APPENDIX 4 (continued)

Acanthocephalans	*Fillicollis anatis* *Polymorphus minutus*

* Also found from the Paradise Shelduck *T. variegata* during the present study.